THE MECHANISMS AND CONSEQUENCES OF CEREBRAL LATERALIZATION

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Abstract

There is a clearly established division of functional processing between left and right hemispheres of the brain, with the pattern showing robust consistency across individuals. The finding of functional differences between the hemispheres of the brain raises two important questions: First, what mechanisms gave rise to the lateralized biases in processing function? Second, what are the consequences of functional asymmetry of cognitive processing in the human brain on our everyday behaviour? Examining the mechanisms that give rise to cerebral lateralization, Experiments 1 and 2 tested the assumption that there is a causal relationship in the degree and direction of lateralization between left- and right-hemisphere dominant tasks. In experiment 1, this relationship between left-hemisphere processing of speech sounds and right-hemisphere processing of emotional vocalizations was examined using dichotic listening tasks. An overall complementary pattern of lateralization was observed across participants, but no significant relationship was found for degree of lateralization of speech and emotional vocalization processing within individuals. These results support the view that functions in the left and right hemispheres are independently lateralized. In Experiment 2 we examined the relationship pattern in degree of lateralization between linguistic processing and melody recognition using dichotic-listening tasks. The expected left-hemisphere advantage was observed for the linguistic processing task, but the expected right-hemisphere advantage was not observed for the melody recognition task, precluding an informative assessment of complementarity between the two tasks.

The division of processing between the two hemispheres of the brain has been shown to result in lateralized performance advantages and behavioural biases. Examining

these consequences of lateralization, Experiments 3 through 6 explored the influence of lateral biases on everyday behaviour. Experiments 3 and 4 examined the influence of asymmetries in facial attractiveness on posing biases. Despite evidence suggesting that the right side of the face is found to be more attractive, professional modeling photographs examined in Experiment 3 revealed a leftward posing bias suggesting that asymmetries in facial attractiveness are not dominant in influencing posing behaviour, even when the purpose of the image is to highlight attractiveness. Experiment 4 controlled for image selection biases by examining posing behaviour directly and revealed a rightward posing bias when participants were asked to emphasize their attractiveness. Experiments 5 and 6 examined the influence of lateralized cognitive processing demands on seating preferences. Experiment 5 investigated the real-world seating patterns of theatre patrons during actual film screenings. It was found that, when processing expectations relied on right-hemisphere dominant processes, such as emotional, facial, or visuospatial processing, people were more likely to choose a seat to the right side of the room. Experiment 6 was designed to test two competing theories that have attempted to explain seating biases: one posits that expectation of processing demand drives the bias; the other posits that basic motor asymmetries drive the bias. Through naturalistic observation, I recorded classroom-seating choices of university students using photographs. When processing expectations relied on left-hemisphere dominant processes, such as linguistic processing, people were more likely to choose seats on the left side of the classroom; this finding contrasts the right side bias observed in theatre seating studies, providing evidence that expectation of processing demands influences the seating bias.

Addressing the mechanisms that guide the evolution of lateralization, no support for the assumption of a causal relationship between complementary left-and right-lateralized cognitive functions was found. Additionally, examination of asymmetries in everyday behaviours such as seating and posing provide evidence that the lateralization of cognitive functions has a direct influence on human behaviour and interaction with the environment.

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Dedication

For my Dad.
You always knew when to push and when to encourage.
I wish you could have read this.

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1. The Mechanisms and Consequences of Cerebral Lateralization

There is now a clear body of evidence supporting a division of processing functions between the left and right hemispheres of the brain (Corballis, 1991; Deppe et al., 2000; Knopman, Rubens, Klassen, Meyer, & Niccum, 1980; Sperry, 1982). Although research is plentiful in determining which structures and functions are asymmetrically lateralized, there are still unanswered questions regarding the nature and origins of cerebral laterality (Bryden, 1990). How and why did cerebral laterality arise? Why do we see individual differences in lateralization? What influence does cerebral lateralization have over how we interact with the world? These questions can be reduced to two foundational aspects of laterality: 1) Mechanisms – how and why did the typical pattern of cerebral lateralization arise? 2) Consequences – what are the influences of this lateralized pattern of functioning on everyday behaviour? In this thesis, I will examine both the underlying assumptions of the theorized mechanisms of cerebral lateralization and the consequences of lateralized cognitive functioning on real-world behaviour.

1.1 Structural Asymmetries

Substantial differences in specific neuroanatomical structures have been noted between the two hemispheres of the brain. In general, the right hemisphere is larger, both in terms of volume and weight (Gur, et al., 1991; Kertesz, Black, Polk, & Howell, 1986), yet the left hemisphere shows a greater overall cell density (Miller, 1996). Likely contributing to the greater cell density, the left hemisphere of the brain has been shown to contain a higher proportion of grey matter relative to white matter compared to the right hemisphere (Gur et al., 1980). Another general asymmetry noted in the brain is the right frontal and left occipital petalia, where the frontal pole of the left hemisphere extends

further forward then the right hemisphere homologue; this pattern is reversed for the occipital pole, where the right hemisphere occipital pole extends further backward than the left hemisphere homologue (LeMay, 1976; see Toga & Thompson, 2003 for a review).

Beyond the general left-right differences, asymmetries are also found within specific structures of the brain. Perhaps the most noted asymmetry is that of the planum temporale. This superior temporal lobe structure has been shown to be significantly larger on the left side of the brain for 65 percent of studied samples (Geschwind & Levitsky, 1968; Chiarello, Vazquez, Felton, & Leonard, 2013). In addition to the planum temporale, the Sylvian fissure extends further horizontally in the left hemisphere than it does in the right hemisphere (Witelson & Kigar, 1992). Other examples of structural differences that favour the left hemisphere include greater white matter volume in Heschl's gyrus (Penhune, Zatorre, MacDonald, & Evans, 1996), larger globus pallidus (Kooistra & Heilman, 1988), and greater volume of the lateral posterior nucleus of the thalamus (Eidelberg & Galaburda, 1982). Consistent and robust leftward asymmetries in both volume and surface area have also been found for the anterior insula, pars opercularis, and pars triangularis (Chiarello *et al.,* 2013).

Not all structures favour the left hemisphere. Some noted examples of rightward structural asymmetries include a deeper and larger central sulcus (Davatzikos & Bryan, 2002), larger anterior cingulate cortex (Pujol et al., 2002), larger posterior insula (Chiarello, *et al*, 2013), and a greater volume of the medial geniculate nucleus of the thalamus (Eidelberg & Galaburda, 1982). A recent finding has demonstrated a rightward volume asymmetry in a wide variety of heteromodal association areas including

inferoparietal cortex, lateral prefrontal cortex, and occipital cortex (Goldberg, et al., 2013).

1.2 Functional Asymmetries

In addition to hemispheric asymmetries in the neuroanatomical structure of the brain, there are also noted hemispheric asymmetries in functional processing within the brain. One of the earliest observations of functional asymmetry in the brain came from Paul Broca's examinations of lesion patients in the 1860s (Broca, 1861). The connection he observed between the occurrence of left frontal lesions and more severe impairment of language production suggested a lateral bias in speech processing; shortly afterward, Wernicke (1874) produced evidence of a similar association between left temporal lobe damage and impairment in speech comprehension. Together these observations laid the foundation for an extensive body of research examining the functional differences between the hemispheres.

In the healthy brain, a set of white matter commissures, including the corpus callosum, anterior commissure, and posterior commissure, shuttle information back and forth between the two hemispheres, allowing the two halves of the brain to communicate and function as a whole. When those commissures are severed, the two halves become isolated. Cases of complete hemispheric disconnection are rare, but corpus callosotomy patients, those who have had the corpus callosum severed but retain some interhemispheric connections via the posterior and anterior commissures, provide an opportunity to examine the two hemispheres with the majority of the interhemispheric communication pathways disconnected. In the 1960s, Roger Sperry examined a group of corpus callosotomy patients to observe the functional abilities of each of the hemispheres

in relative isolation. His work not only supported the earlier finding of a left-hemisphere dominance for language processing, it also revealed a right-hemisphere dominance for other functions including visuospatial processing (Gazzaniga, 1967; Sperry, 1968; 1982) and face processing (Levy, Trevarthen, & Sperry, 1972; Sperry, 1974).

Subsequent research on both patient and neurologically healthy populations has provided evidence of a variety of processing asymmetries between the two hemispheres. For example, the left hemisphere excels at linguistic processing (Kimura, 1961), rhythm and temporal processing (Sakai, et al., 1999), mathematical information processing (Pinel & Dehaene, 2010), and analytical processing (Bever, 1975). The right hemisphere excels at processing prosody (Grimshaw, 1998), visuospatial processing (Bryden, 1982), facial recognition (Levy et al., 1972), and emotional processing (Bryden & MacRae, 1989; Suberi & McKeever, 1977; but see Demaree, Everhart, Youngstrom, & Harrison, 2005 for a review and counterargument). This generally consistent pattern of cerebral lateralization that has emerged suggests distinct and complementary processing roles for the left and right hemispheres of the brain across individuals. Bryden (1990) coined this pattern the Modal Model.

1.3 Mechanisms

The finding of functional differences between the hemispheres of the brain raises two important questions: First, what generates the lateralized biases in processing function? Second, why did these asymmetries arise? Together, these questions address the mechanisms of functional lateralization.

The first question asks what physiological mechanism drives the observed pattern of lateralization. A genetic component to human laterality is strongly supported, with

handedness providing the key example. McManus and Bryden (1992) conducted a meta-analysis of studies examining the heritability of handedness and found that the incidence of left-handedness is strongly related to the handedness of the parent. For two right-handed parents, the chance of a child being left-handed sits at 9.5%; when one parent is left-handed, the chances of producing a left-handed child increase to 19.5% and rise further to 26.1% when both parents are left-handed. These results do not distinguish between the influence of biological or genetic control and environmental influences, as behaviour such as handedness may be learned from the parents. To tease apart the environmental and behavioural influences, Hicks and Kinsbourne (1976) examined the correlation of student handedness with that of their biological and step-parents. Providing evidence against environmental influence, they found that student handedness was predicted only by the handedness of the biological parent. A subsequent adoption study provided further evidence that it is the handedness of the biological parent, and not the adoptive parent, that predicts a child's handedness (Carter-Saltzman, 1980).

1.3.1 Genetic Theories of Handedness

Genetic theories of handedness provide a foundational mechanism for the incidence of handedness; they provide a concrete explanation for how patterns of lateralization are determined. Although genetic theories of laterality focus mainly on handedness, two notable examples attempt to extend the genetic explanation to language lateralization as well.

1.3.1.1 Right Shift Theory.

Annett (1972;1985) proposed the influence of a right shift gene on brain organization. A single gene comprised of two inherited alleles is posited to influence

handedness and language lateralization. The allele of the right shift gene (RS+) drives the development and organization of the motor and speech processing systems in the left hemisphere of the brain. The bias introduced by this RS+ gene results in a rightward motor skill bias (right shift). A second allele of the right shift gene (RS-) is indifferent to direction of lateralization. Rather than resulting in a leftward shift, the RS- allele leaves direction of lateralization to chance. With the two alleles, three possible heritability patterns emerge: RS+RS+, RS+RS-, and RS-RS-. The presence of the RS+ allele biases the developmental trajectory towards right-handedness, with the strength of the bias positively related to the number of RS+ alleles inherited. As the majority of people will receive at least one RS+ gene, a right shift for motor skill (right-handedness) will be observed for most people. Those people with the RS-RS- genotype will show fluctuating asymmetry, with half the individuals being right-hand dominant and the other half being left-hand dominant.

When the probabilities of handedness are calculated, the Right Shift Theory predictions closely match the observed heritability rates of handedness (Annett 1983; Annett, 1985). In addition, the proposed influence of the right shift on both motor and speech processing regions provides a link between the lateralization of handedness and functional processes.

1.3.1.2 McManus' (1985) Genetic Model.

A similar theory to Annett's Right Shift Theory was proposed by McManus (1985). Like Annett, McManus proposed a two-allele model where one allele (D) codes for right-handedness (Dextral), and a second allele (C) codes not for left-handedness but for chance determination of hand preference. Again, three possible heritability patterns

are possible: DD, DC, CC; the predicted rate of right-handedness is positively related to the number of D alleles present. The incidence rate for right-handedness in people with the CC genotype is chance (50%) and rises to 75% for people with the DC genotype; the incidence rate finally rises to 100% for people with DD genotype. McManus's model also accounts for the lateral bias observed for language processing; the C and D alleles control the incidence rates for language processing in the same manner as they dictate hand preference, with the D allele biasing language lateralization to the left hemisphere of the brain (McManus, 1999).

1.3.2 Evolutionary Theories of Lateralization

Although genetic theories provide a strong candidate for the foundational mechanism that generates the lateralized patterns we observe, providing an explanation for what drives the biases we observe, they do not explain why these biases in lateral asymmetry arose, or what adaptive purpose they serve. Several theories have been proposed to address the question of why lateral asymmetries evolved and what adaptive function they serve.

1.3.2.1 Evolution of fine motor skill.

In an attempt to reconcile the relationship between handedness and language lateralization, Corballis (1991) proposed that tool use and refinement in early hominids resulted in increased motor control and fine motor skill. As the fine motor skills became more refined the neural control of fine motor programming shifted from bilateral involvement in fine motor control to left-hemisphere specialization for fine motor programming. This left-hemisphere bias is associated with right-hand dominance as the left hemisphere motor cortex controls motor functioning for the right side limbs. Further,

Corballis suggests that the fine motor control required to make tools is similar to the motor control required to make the small, rapid motor movements that make speech possible. As such, the regions responsible for processing speech and language are also biased to left-hemisphere control. Although not explicitly stated in Corballis's theory, a corollary to this proposed relationship would be that any functions that did not rely on the left-hemisphere's fine motor control would then be allocated to the right hemisphere.

1.3.2.2 Evolution of rapid motor processing.

Kimura and Archibald (1974) proposed a similar evolutionary explanation of cerebral lateralization. Rather than positing a specialization for fine motor control, they suggested that a left-hemisphere superiority for processing complex and rapid temporal motor sequences evolved from right-hand dominance in tool use. These complex sequencing skills provided a motor framework that supports the complex sequential movements required for the production of both gestural and spoken communication.

1.3.2.3 Postural Origins Theory.

Relying on a different lateralizing influence, MacNeilage (1991; 1998) prosed that the vertical clinging position required in the arboreal environment resulted in a lateral asymmetry in postural control. A left-hand dominance for predation in primates emerged as a result of a right-side dominance for providing postural support in the arboreal environment. While foraging for insects and small animal prey, primates tend to use the right arm to grasp the branch, and the left arm to reach for the food.

As a result of this foraging and predation pattern, the left and right hemispheres became specialized for complementary activities: the left-hand dominance in predation lead to a right-hemisphere dominance for visuospatial processing as left hand reaching

and targeting skills evolved. Conversely, the right-side postural support bias resulted in the development of a left-hemisphere dominance for whole-body postural support. As a consequence, the left-hemisphere was suited to provide the body stability needed to support the lung and glottis motions used to produce speech (MacNeilage, 2007). This model extends beyond the handedness-language relationship to include lateralization of visuospatial processing in an attempt to more fully account for the modal model of functional laterality.

1.2.3.4 Computational Theory.

Like MacNeilage (2007), Kosslyn (1987) proposed a theory that directly accounted for the distinct functional asymmetries in left and right hemispheres. He posited that the coordination of rapid, temporally ordered sequences of processing operations required a degree of coordination that could not be adequately achieved with bilateral processing control. As processing sequences became more complex, a lateral bias evolved to allow for a single set of commands to govern sequential processing coordination across both sides of the body. Further, Kosslyn argued that there were two major control systems operating within the brain: one system controlling the sequencing of speech production (left hemisphere), the other controlling the shifting and orienting of visuospatial attention (right hemisphere). These two systems are most efficient if they are lateralized to opposite hemispheres, otherwise crowding results where language processing takes priority of the processing resources at the expense of visuospatial performance (Levy, 1969). Kosslyn (1987) then argued that the lateral asymmetry of these two systems subsequently biases the lateralization of the other functional systems in

the brain with which they interact, creating an overall complementary pattern of lateralization across all cerebral functions.

1.2.3.5 Interhemispheric Conduction Delay Hypothesis (ICD).

Where the previous theories targeted one or two specific systems as the basis for cerebral lateralization, Ringo, Doty, Demeter, & Simard (1994) suggested that cerebral lateralization broadly represents an evolutionary adaptation to compensate for the increased delay in signal conduction time between the hemispheres as brain size increased. They argue that, for tasks requiring a high degree of temporal precision, the delay in signal conduction time between the right and left hemispheres of larger brains would prevent efficient signal processing and programming of motor responses. By restricting the processing for a specific function or process to a single hemisphere, temporal delays in signal processing are reduced and processing efficiency is improved.

1.3.3 Testing Assumptions – Patterns of Complementarity

With the exception of the ICD hypothesis, all of the evolutionary theories presented here share a common assumption: they posit a causal relationship between the left- and right-lateralized functions. As each theory attempts to account for the modal model's population-level asymmetries, there is an inherent implied or expressed assumption that the asymmetrical lateralization of one function drives the subsequent opposite lateralization of another. This pattern appears to be implied by the modal model, as the measured lateral asymmetries for functions like language and visuospatial processing appear to be consistent and robust.

There is a challenge to the modal model: although the population-level asymmetries are robust and consistent overall, there are some notable exceptions to the

modal model. For example, approximately 95% of right-handed individuals are left-hemisphere dominant for language processing, a figure in keeping with the modal model; however, the incidence rate drops to 70% when language lateralization is examined in left-handed individuals, suggesting 30% of left-handers do not conform to the modal model (Damasio & Damasio, 1992; Springer & Deutsch, 1993). Similarly, when lateralization of language processing is compared across the sexes, males tend to show strong leftward lateralization, whereas women tend towards more bilateral processing rather than strict left hemisphere dominance (Clements et al., 2006). Chiarello, Dronkers, and Hardyck (1984) compared individual performance on a lateralized lexical decision task to the overall group performance and found that, despite a significant right visual field advantage for the group, most individual participants did not show significant asymmetries. These examples suggest that, despite a consistent pattern of population-level biases in functional processing, the modal model may not hold true when patterns of cerebral lateralization are examined at the level of the individual.

Although the modal model appears to imply a causal relationship between left- and right-lateralized functions, there are three possible patterns of complementary organization within-individuals that can give rise to the population-level modal model:

1.3.3.1 Causal complementarity.

Causal complementarity is the pattern that arises if asymmetrical lateralization of one function drives the opposite asymmetrical lateralization of the other function. For example, the modal model presents the left hemisphere as the linguistic side of the brain whereas the right hemisphere is the visuospatial side of the brain (Bryden, 1990). As this pattern predicts opposite lateralization for complementary functions, a negative

correlation in the degree of lateralization between complementary functions would be observed within individuals.

1.3.3.2 Bias complementarity.

Bias complementarity is the pattern that arises if asymmetries of either attention or ascending sensory systems result in an overall bias in processing information (Bryden, 1990). As the bias influences either a complete sensory system or a global attentional mechanism the bias pattern predicts that a strong bias for a left-lateralized function will be accompanied by a weak bias in the same direction for a right-lateralized function (and vice versa); thus, a positive correlation in the degree of lateralization between complementary functions would be observed within individuals.

1.3.3.3 Statistical complementarity.

Statistical complementarity is the pattern that arises if the sources of influence underlying asymmetrical lateralization of complementary functions are independent of one another. Each lateralized function has an independent probability of being biased to a specific hemisphere. As the complementary functions are independently lateralized, there would be no correlation in the degree of lateralization observed within individuals (Bryden, 1990). To assess the validity of the causal complementarity assumption inherent in most evolutionary theories of hemispheric laterality, the pattern of complementarity between left- and right-lateralized functions must be examined within-individuals. For these theories to hold support as plausible mechanisms for the lateralization of cerebral functioning, a causal relationship between complementary functions must be established. Unlike the other four theories discussed, Ringo and colleagues (1994) do not propose a specific direction or pattern of functional lateralization; they do not attempt to account for

the population-level asymmetries observed for language, spatial attention, or emotional processing. Rather, they suggest that probabilistic biases are likely the lateralizing force for each function, and as such, the theory predicts a statistical relationship between complementary functions. Experiments 1 and 2 were designed to assess which pattern of complementarity is observed within individuals for a pair of complementary, lateralized functions.

1.4 Consequences

Evolutionary theories explaining the mechanisms of laterality posit an adaptive advantage to lateralized function in the brain. For some behaviours we can see the direct influence of functional lateralization – handedness is the obvious example. Left hemisphere dominance for fine motor control or for complex sequencing of action is argued to result in a motor asymmetry favouring the right hand in the majority of individuals. Beyond the extensive study of handedness, relatively few studies examine the greater impact of functional asymmetry of cognitive processing in the human brain on real-world behaviour.

1.4.1 Performance Advantages

Sperry's work with split brain patients provided a leap towards understanding the relative functional influences of the two hemispheres of the brain. Their relative contributions could be assessed with careful presentation of stimuli to one hemisphere in isolation. In the neurologically healthy individual it is not possible to test the hemispheres in isolation to see the relative influence of each on behaviour; however, taking advantage of the anatomical asymmetries in the human visual and auditory systems, it is possible to

present information preferentially to one hemisphere and observe whether the speed or accuracy of task performance is influenced by the preferential presentation.

1.4.1.1 Left hemisphere performance advantages.

The influence of the leftward bias in language processing on linguistic task performance has been clearly established in both the auditory and visual modalities. Kimura (1961) presented dichotic pairs of spoken digits to participants and asked them to recall as many digits as they could. A clear accuracy advantage for recalling the digits presented to the right ear was observed; Kimura attributed this advantage to the left hemisphere's dominance for language processing as the majority of auditory projections from the ear cross to the opposite hemisphere of the brain for processing. Similarly, Wexler and Halwes (1983) found participants preferentially selected the word presented to the right ear when asked to select which of four rhyming words were presented during a dichotic listening task.

A similar advantage in accuracy performance emerges when we look at responses to verbal stimuli in the visual domain. Mishkin and Forgays (1952) found a right visual field advantage for recall accuracy when participants were asked to recall letter strings presented to either the right or left side of visual space. As the visual projections from each visual field cross to the opposite hemisphere for processing, the right visual field advantage reflects left hemispheric dominance for linguistic processing (Beaumont, 1983). This right visual field performance advantage replicated an earlier finding by Heron (1957). Later studies revealed reaction time advantages for the right visual field using a lexical decision task, providing evidence that the right side advantage is robust

across language processing tasks (Ibrahim & Eviatar, 2009; Lavidor, Ellis, & Pansky, 2002; see McKeever, 1986 for a review).

In addition to language, left hemisphere performance advantages have also been widely observed for other functions as well. Rapid temporal processing tasks such as the two-flash fusion task (Nicholls, 1994), and gap detection tasks, both auditory (Brown & Nicholls, 1997) and visual (Okubo & Nicholls, 2008), have shown consistent left hemisphere processing advantages (Nicholls, 1996). The left hemisphere also shows a processing advantage for processing the local details of visual objects, with participants showing faster and more accurate identification of local pattern elements in hierarchical stimuli presented to the right visual field (van Kleeek, 1989). Finally, a right ear accuracy advantage has been found for identifying melodic sequences that differ only in rhythm (Gordon, 1978).

1.4.1.2 Right hemisphere performance advantages.

Although less robust and consistent than the left-hemisphere advantage found for language processing, several right-hemisphere processing asymmetries have been well established in the literature. Emotion is one of the most studied right-lateralized functions, and processing advantages for emotional content have been found for both the auditory and visual modalities. In the auditory domain a consistent left ear advantage for accuracy in identifying the emotion intonation of speech has been found (Bryden & MacRae, 1989; Buhlman-Fleming & Bryden, 1994; Ley & Bryden, 1982). Using a similar dichotic presentation, both King and Kimura (1972) and Carmon and Nachshon (1973) found that the left ear advantage for accurate identification of emotional content extended to non-linguistic emotional sounds such as crying or laughter.

In the visual modality, a left visual field advantage has repeatedly been found for emotional facial expressions, with performance advantages observed for both accuracy and reaction time (McKeever & Dixon, 1977; Suberi & McKeever, 1977); however, facial processing is also shown to be asymmetrically lateralized to the right hemisphere, resulting in left visual field advantages for facial recognition tasks using emotionally neutral faces (Cohen Leehey & Cahn, 1979; Wolff, 1933). As such, the use of face stimuli to measure emotional processing begs the question: is the performance advantage due to facial processing, emotional processing, or both? Attempts to dissociate the two processes have lead to mixed results. Suberi and McKeever (1977) used emotional and neutral faces to examine processing advantages for both facial identity and emotional processing. Participants were asked to memorize either an emotional or neutral target face and indicate whether the face presented tachistoscopically matched the assigned target. They found a greater left visual field advantage for emotional target identification performance than for neutral face identification performance. Safer (1981) found the opposite pattern using a similar procedure; participants showed a greater left visual field advantage for facial identification than for emotional identification. Ley and Bryden (1979) presented pairs of faces to participants and asked them to judge whether the faces were the same or different based on either emotional expression or facial identity. They found similar left visual field advantages in performance accuracy for both tasks. Although the relative contribution of facial and emotional processing to the left visual field performance advantage in tasks using facial stimuli is unclear, both faces and emotions show strong evidence of right hemisphere performance advantages.

Although not a processing advantage, per se, performance on visuospatial tasks tend to show consistent leftward biases. For example, when presented with a single horizontal line and asked to bisect the line through the center, neurologically healthy individuals will bisect the line slightly to the left of center (Jewell & McCourt, 2000). Similarly, when Nicholls, Bradshaw, and Mattingley (1999) asked participants to judge paired sets of stimuli on the relative brightness, numerosity, or size, a consistent bias to choose the stimulus with the feature being judged presented on the left side of visual space. For example, participants were presented with a pair of horizontal bars, each containing an equal number of stars; one featured a greater density of stars on the left side of the bar, the other featured a greater density of stars on the right side of the bar. When asked which bar appeared to have a greater number of stars, participants selected the bar with more stars on the left more often than they chose the bar with more stars on the right. These systematic leftward biases have been consistently observed across a variety of spatial tasks (Bowers and Heilman, 1980; Heilman, Bowers and Watson, 1984; Bradshaw and Nettleton, 1983; Bradshaw, Nettleton, Nathan & Wilson, 1985; Milner, Harvey, Roberts & Forster, 1993; Chieffi, 1996; McCourt and Olafson, 1997; McCourt and Jewell, 1999; McCourt and Garlinghouse, 2000).

1.4.2 Influence on Real-world Behaviour

There are clear influences on task performance related to hemispheric lateralization of cognitive processes, yet few studies have examined how these lateralized processing and behavioural biases affect everyday, real-life behaviours. If the evolutionary theories of lateralization are correct, and the development of skilled movements and unimanual behaviours influenced the lateralization of processing

functions in the human brain, then it would follow that we should see asymmetries in everyday behaviours as a function of that asymmetry.

Language dominance has received the most attention, and it has been shown to influence a number of behaviours from how we hold the phone during a conversation (Seidman, Seigel, Shah, & Bowyer, 2013), to how we orient our head and body position during a conversation in a crowded environment (Marzoli & Tommasi, 2009). Other studies have demonstrated an influence of right side motor biases on the direction we turn when entering a room (Scharine & McBeath, 2002), and the direction of head tilt when kissing a loved one (Barrett, Greenwood, & McCullagh, 2006). Additional studies have explored the influence of hemispheric asymmetries on seating (Nicholls, Thomas, & Loetscher, 2013) and posing (Nicholls, Clode, Wood, & Wood, 1999). Experiments 3 through 6 were designed to test the influence of lateralized cerebral processing demands on real-world behaviours.

2. Experiment 1: Examination of Complementarity in Speech and Emotional Vocalization Perception[1]

Clear evidence exists for a division in cognitive functioning between the left and right hemispheres of the brain (Corballis, 1991; Sperry, 1982). It is argued that this division of processing enables more efficient processing of information, as each hemisphere is specialized for specific information input (Bradshaw, 2001; Levy, 1977). Coined the Modal Model by Bryden (1990), the left hemisphere is often thought of as the language center, as well as an analytic and serial processor responsible for coordinating rapid, sequential processing tasks. In contrast, the right hemisphere is thought of as the visuospatial and emotional center, as well as an holistic and integrative processor, responsible for parallel processing of information.

Stemming from this view, the left and right hemispheres of the brain are largely thought to play complementary roles in cognitive processing (Hellige, 1993). Left-hemisphere dominance for language processing has been long established (Broca, 1861; Hecaen, DeAgostini, & Monzon-Montes, 1981; Kimura, 1961). Despite an historical reputation as the emotional perception hemisphere, evidence regarding the lateralization of emotional processing is divided, suggesting a complex processing network (Wagner, Phan, Liberzon, & Taylor, 2003). Evidence for right-hemisphere dominance in perceiving emotional stimuli comes from tachistoscopic studies using emotional faces (McKeever & Dixon, 1971; Suberi & McKeever, 1977) as well as dichotic-listening studies, which employ the simultaneous presentation of different auditory stimuli to each ear, using

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emotional intonation (Bryden & MacRae, 1989; Bulman-Fleming & Bryden, 1994) in neurologically healthy populations.

Although evidence from visual-field and dichotic-listening studies provide consistent evidence of right-hemisphere dominance in emotional perception and processing, it has been argued that the left hemisphere also plays a role in emotional processing, particularly in the expression and experience of emotions. The Valence Hypothesis (Ahern & Schwartz, 1979) and the Valence-arousal Hypothesis (Heller, 1993) both posit a dual hemisphere processing of emotional information, with the right hemisphere processing negative or withdrawal emotions and the left hemisphere processing positive or approach emotions. Davidson (1984; 1992) proposed a modified variant of the Valence Hypothesis wherein he posits a similar right- and left-hemisphere division for expression and experience of actual emotion, but argues for a right-hemisphere dominance for the perceptual processing of emotional stimuli (for a detailed review see Demaree, Everhart, Youngstrom, & Harrison, 2005). Evidence in support of a left-hemisphere role in emotional expression has been found in studies of patients with unilateral brain damage. Patients with left-hemisphere lesions are more likely to experience depression following injury than patients with right-hemisphere lesions (Robinson & Price, 1982). Conversely, patients with right-hemisphere lesions are more likely to experience positive changes in mood than patients with left-hemisphere lesions (Sackheim, et al., 1982). A similar pattern has been observed in patients undergoing sodium amytal testing, with left carotid artery injections resulting in a dramatic negative emotional experience (e.g. crying, pessimistic thoughts, and worry); right carotid artery injections resulted in a dramatic positive emotional experience (laughter, smiling, general

euphoria; Perria, Rosadini, & Rossi, 1961; Rossi & Rosadini, 1967; Terzian, 1964). With regard to emotional perception, research indicates a greater deficit in the perception of negative emotions following right hemisphere damage, with little or no deficit in emotional perception following left-hemisphere damage (Adolphs, Damasio, Tranel, & Damasio, 1996; Borod et al., 1998). This evidence suggests a division of processing between the left and right hemispheres for the expression and experience of positive and negative emotions, respectively.

Neuroimaging evidence has provided mixed support for both right-hemispheric dominance and the valence model of emotional processing. Kilgore and Yurgelun-Todd (2007) found greater right-hemisphere activation for emotional facial expressions regardless of valence, with even greater right-hemisphere activation in response to negative emotional expressions. The left hemisphere showed less overall activation in response to emotional expressions, and positive emotional expressions revealed bilateral activation. Wager, Phan, Liberzon, and Taylor (2003) conducted meta-analysis of 65 studies imaging brain activation during emotional processing and found no evidence of greater right-hemisphere activation overall; although no clear support was found for any model of emotional lateralization, the general pattern of activation was more closely aligned with the approach-withdrawal account than the valence model or the right-hemisphere model.

A more consistent pattern highlighting the right hemisphere's emotional dominance emerges for the perception of paralinguistic information (Belin, Zatorre, & Ahad, 2002; Friederici & Alter, 2004; Poeppel, 2003; for a review see Lindell, 2006). These features include prosody (Blonder, Bowers, & Heilman, 1991; Ley & Bryden,

1982; Grimshaw, 1998) as well as non-linguistic emotional vocalizations (such as sighing or laughing; Carmon & Nachshon, 1973; King & Kimura, 1972; Poyatos, 2002; Trager, 1958).

These population-level biases in linguistic and paralinguistic-emotional processing suggest a complementary organization of these two functions within the brain. There is a left-hemisphere bias for linguistic processing and a right-hemisphere bias for emotional perception at the population level when examined between participants; however, what is still unclear is how these two asymmetrical functions are organized within individuals: does the complementary pattern observed across individuals still hold when examining the relationship in degree and direction of lateralization of left- and right-lateralized functions within individuals, or does a different pattern emerge?

When examining the relationship between the asymmetrical lateralization of two complementary functions within individuals there are three possible patterns that can be observed. First is a causal pattern of complementarity (Bryden, 1990; Bryden, Hecane, & DeAgostini, 1983). Here, it is argued that the asymmetrical lateralization of one function drives the opposite asymmetrical lateralization of the other function. For example, the modal model presents the left hemisphere as the linguistic side of the brain whereas the right hemisphere is the visuospatial side of the brain. MacNeilage (1991) proposed a theory of language lateralization suggesting that a right-hemisphere visuospatial bias guiding predation resulted in the left hemisphere governing postural support. This left-hemisphere postural bias provided the necessary framework upon which language processing and production abilities were developed. If the right hemisphere is specialized for the processing demands of visuospatial processing, the left hemisphere will then be

driven to specialization for the processing demands of linguistic processing. Further, this position would also predict that, in the case where the left hemisphere becomes specialized for visuospatial processing, the right hemisphere would then become specialized for linguistic processing. As this pattern predicts that complementary functions should be opposite in lateralization, a negative correlation in the degree of lateralization between the complementary functions should be observed.

The second pattern is a bias pattern of complementarity (Bryden, 1990). Here, it is argued that asymmetries of either attention or ascending sensory systems result in an overall bias in processing information. In the former case it argued that an overall attentional bias to right-side stimuli would produce a large right ear advantage (REA) for a linguistic task and a smaller REA for a non-verbal emotional processing task (Efron, Koss, & Yund, 1983; Kinsbourne, 1975). Similarly, an asymmetry in the ascending sensory systems would result in an overall bias within each sensory system. As such, a right-side auditory asymmetry would result in a large (REA) for a linguistic task and a smaller REA for a non-verbal emotional processing task (Sidtis, 1982; Teng, 1981). Contrary to the causal pattern, bias complementarity does not predict that complementary functions be lateralized to opposite hemispheres. Rather, complementary functions would be more likely to be asymmetrically lateralized within the same hemisphere; thus, a positive correlation in the degree of lateralization between the two functions should be observed.

The third pattern is a statistical pattern of complementarity (Bryden 1982; Bryden 1990; Bryden, Hecaen, & DeAgostini, 1983). Here, the sources of influence underlying asymmetrical lateralization of complementary functions are independent of one another.

Each function has an independent statistical probability of being lateralized to a specific hemisphere based on the source of influence driving its lateralization. For example, the underlying influence biasing linguistic processing to be asymmetrically lateralized to the left hemisphere is unrelated to the underlying influence biasing emotional processing to be asymmetrically lateralized to the right hemisphere. Although the population-level pattern observed may appear causal in nature, examination of the relationship between the degree of lateralization for two statistically independent complementary functions should result in no correlation being observed.

There are few studies in the literature that have directly measured the correlation in degree and direction of lateralization between left-hemisphere and right-hemisphere lateralized tasks within individuals. Ley and Bryden (1982) examined the relationship between linguistic and emotional processing using sentence stimuli presented in different emotional tones. Although they observed the expected REA for the linguistic sentence stimuli and a LEA for the emotional content, when the relationship between the two lateralized tasks was examined, no significant correlation was observed. Ley and Bryden (1982) suggested that this result supports the statistical model of complementarity. Similarly, Saxby and Bryden (1984) assessed the complementarity of emotional and linguistic processing in children using the same method as Ley and Bryden (1982); they also found no significant relationship in the degree and direction of lateralization for linguistic and emotional processing, further suggesting a statistical pattern of complementarity between these processes. McNeely and Parlow (2001) examined the complementarity of linguistic and prosodic processing using the Fused Words Dichotic-listening Task (FWDT) and the Dichotic Emotion Recognition Test (DERT). They

observed the expected overall REA for linguistic processing and LEA for prosodic processing at the population level, but no significant correlation was found between the two functions when examined within individuals. More broadly, Andresen and Marsolek (2005) examined the relationship in degree and direction of lateralization for right- and left-hemisphere lateralized shape-recognition and spatial-relation tasks within individuals and found no relationship between the left-hemisphere and right-hemisphere lateralized tasks.

Support for statistical complementarity has also come from recent studies using functional transcranial Doppler (fTCD) to measure lateral differences in cerebral blood flow. Whitehouse and Bishop (2009) used fTCD laterality indices (LI) to examine the relationship in degree and direction of lateralization between visuospatial memory and linguistic processing and found no significant correlation between the LIs for both tasks. Similarly, Rosch, Bishop, and Badcock (2012) found no correlation between fTCD LIs measured for a word generation and a visuospatial landmark task.

Not all research in this area has found support for statistical complementarity. At this time, two studies have provided evidence against statistical complementarity. In the first discrepant finding, Elias, Bulman-Fleming, and Guylee (1999) recruited participants with atypical laterality profiles and the relationship between lateralized linguistic and prosodic processing within these individuals. They found the expected population-level laterality effects for the linguistic and prosodic processing tasks: an overall REA for linguistic processing and an overall LEA for prosodic processing. Contrary to prior research, they found a significant positive correlation in degree and direction of lateralization between the two tasks, suggesting bias complementarity. In the other

discrepant finding, Badzakova-Trajkov, Haberling, Roberts, and Corballis (2010) used functional magnetic resonance imaging (fMRI) to examine the lateralization of face, linguistic, and visuospatial processing. They found significant negative correlations observed between LIs for word generation and LIs for both emotional facial processing and visuospatial processing, providing partial support for causal complementarity. A non-significant positive correlation was observed between the LIs for emotional face processing and visuospatial processing. The authors suggested that these results provide evidence for the influence of multiple lateralizing influences rather than a single lateralizing force.

In this study, I specifically examined the pattern of relationship between the perception of speech and the perception of non-linguistic emotional vocalizations within-subjects. Non-linguistic emotional sounds were chosen for this study to allow for the separation of paralinguistic information from any linguistic processing. Using asymmetry scores obtained using both a speech task and an emotional vocalizations task, we examined the pattern of lateralization observed for each task in the overall sample. We also examined the relationship in the degree and direction of lateralization for speech processing and for non-linguistic emotional vocalization processing within-subjects in order to assess which of the above patterns of complementarity is observed for these asymmetrically lateralized functions. If the general assumption that the modal model reflects a causal relationship between left- and right-lateralized functions is accurate, then we should observe a significant negative correlation. If an attentional or sensory system bias is governing these lateralized processes, then we should observe a significant positive correlation. Finally, if independent processes are responsible for the

lateralization of each of these left-and right-lateralized processes, then no correlation in the laterality scores should be observed.

2.1 Method

2.1.1 Participants

Fifty-two (11 males and 41 females) neurologically healthy undergraduate students from the University of Saskatchewan participated in the present study for course credit (mean age 20.40, *SD* = 4.65). All participants were right-handed as assessed by the short version of the Waterloo Handedness Questionnaire – Revised (Elias, Bryden, & Bulman-Fleming, 1998; mean = 21.62, *SD* = 4.33). All participants reported normal hearing with no history of hearing loss. The data from one female participant was excluded because of reported temporal lobe epilepsy.

2. 1.2 Materials

2.1.2.1 Fused Rhymed Words Test.

Lateralization for speech processing was assessed using the Fused Rhymed Words Test (FRWT; Wexler & Halwes, 1983). The test consists of 15 dichotic pairs of rhymed words that differ on initial phoneme (e.g. boy-toy). The simultaneous presentation of these words results in a fusing of the two words, such that one word is typically perceived. Each pair of rhyming stimuli was presented 16 times (eight times on each channel) for a total of 240 trials. The trials were divided into two main blocks of 120 trials each (Block A and Block B). Each main block was further divided into four blocks of 30 trials. The stimuli were played off a CD using Windows Media Player through Sennheiser headphones (model HD-437). Participants were presented with an answer

booklet and were asked to circle which word was heard from a list of four possible choices.

2.1.2.2 Emotional Sounds Task.

Lateralization for emotional vocalization perception was assessed using an emotional sounds task (EST) designed for the present study. King and Kimura (1972) used non-lingusitic emotional sounds in a dichotic listening task to assess lateralization of emotional processing and found a significant LEA. In their study, participants were presented with a dichotic pair of emotional sounds (e.g. crying and sighing) and were then asked to identify the two sounds presented from a set of four options presented binaurally. As it has been argued that the memory load for such a task may influence performance (Bryden, 1982), we used the same stimuli but altered the response procedure. A stimulus set was created using non-linguistic emotional sounds (e.g. growling, gasping, sighing, and moaning). Fifteen emotional sounds were downloaded from public access sound effects websites; an additional three sounds were recorded using Audition (Adobe) for a total of 18 sounds (sampling rate: 44.1 KHz, resolution: 16 bit); nine positive emotions (e.g. laugher and cheering) and nine negative emotions (e.g. crying and screaming) were sampled. The sounds were played for 10 observers who were asked to indicate whether the sound matched the emotional label assigned to it. Out of the 18 total sounds, 12 sounds were unanimously rated as matching their assigned emotional label and were used to create the task. All sounds were edited to a common length of 1000ms and were equalized for intensity. Each emotional token was paired dichotically with every other token to produce 132 emotional sound pairs. The sound pairs were presented using E-prime (Psychology Software Tools). In order to assess the

influence of valence effects, one positive ("content") emotional sound and one negative ("depressed") emotional sound were chosen from the 12 tokens as the target sounds for the task.

2.1.3 Procedure

Participants were tested individually. Once informed consent was provided, participants filled out a demographics questionnaire that assessed handedness and footedness (Elias et al., 1998) and addressed sex, age, and vision or hearing impairments. Once the questionnaire was completed, participants completed the FRWT and EST, counterbalanced for order of presentation. All tests were completed in a single session lasting approximately one hour.

2.1.3.1 FRWT.

The participants were seated at a table and given a response booklet to record their responses on the task. Following an explanation of the nature of the dichotic listening task, participants completed 30 practice trials. Each of the 30 words used to create the rhymed pairs was presented once, binaurally. Participants were asked to circle which word was heard in the response booklet. The practice trials were then followed by the test trials. Participants were asked to respond as quickly and as accurately as possible. Word pairs were presented with an interstimulus interval of 2.5 seconds. Participants were given a brief break after each block of 30 word pairs before beginning the next block of trials. The position of the headphones was reversed four times throughout the task (after blocks 1, 3, 5, and 7).

2.1.3.2 EST.

Unlike the FRWT, which was administered using a CD with participants providing their responses with pen and paper, the EST is a computer-based task. Participants were seated in front of the computer and were instructed to listen for a target emotional sound ("content" or "depressed"). They were then asked to listen to each of the 12 emotional sound tokens while reading the associated emotional label on the computer screen to familiarize them with their target emotional sound. Next, the participants completed 26 practice trials. They were instructed to rest the index and middle fingers of their right hand on the 'y' and 'u' keys. Each of the sound tokens was then presented binaurally and the participants were asked to indicate whether their target emotional sound was present by pressing either the yes key (y) or the no key (u) on the keyboard. Participants were asked to respond as quickly and as accurately as possible. Upon completion of the practice trials, the participants were instructed to press the space bar to begin the test trials. The computer monitor then displayed a black screen while the sound pair was presented. Immediately following presentation of a dichotic emotional sound pair participants were presented with a visual message prompting them to indicate whether they heard the target emotional sound ("yes or no?"). A response prompted the start of the next trial. After the first block of trials was completed, participants were instructed to listen for the other target emotional sound; the procedure was repeated. Order of emotional targets was counterbalanced between participants.

2.1.3.3 Calculation of asymmetry scores.

The data from the FWRT and EST were converted to lambda (λ) scores, as described by Bryden and Sprott (1981):

$$= \ln\left(\frac{(\text{REcorrect} + .005)(\text{LEincorrect} + .005)}{(\text{LEcorrect} + .005)(\text{REincorrect} + .005)}\right)$$

Where RE indicates right ear responses and LE indicates left ear responses. This measure of degree of lateralization, based on the log-odds ratio, provides a measure of lateralization that is approximately normal in its distribution and is not dependent on overall performance. Positive λ values reflect a right-ear performance advantage (REA).

2.2 Results

2.2.1 FRWT

The FRWT elicited the expected REA in 90% of participants (46/51). One participant exhibited no ear advantage on the task. This observed overall REA was significant, $t(50) = 8.122$, $p < .001$ ($M = .285$, $SD = .251$). Performance did not differ between Block A and Block B of the task, $t(50) = .978$, $p = .333$. A one-sample *t*-test examining overall accuracy revealed that performance on the task was above chance levels, $t(50) = 93.206$, $p < .001$ (chance = 120, $M = 230.02$, $SD = 8.42$).

2.2.2 EST

A paired-samples *t*-test revealed no influence of block on performance accuracy for the task, $t(50) = -.231$, $p = .818$, so data was collapsed across blocks for the remaining analyses. A 2 x 2 ANOVA examining the influence of target (content, depressed) and ear (left, right) on performance accuracy revealed no main effect of target, $F(1,50) = .16$, $p = .691$, and no main effect of ear, $F(1, 50) = 2.27$, $p = .138$. The interaction was not significant, $F(1, 50) = .84$, $p = .363$. When the λ values were examined, the EST elicited the expected LEA in 55% of participants (28/51). Nine participants did not elicit any ear advantage on the task. The observed overall LEA was not significant, $t(50) = -1.580$, $p =$

.120 (*M* = -.313, *SD* = 1.415). As approximately half of the participants performed at 100% accuracy for one or both blocks of trials, it is possible that ceiling performance effects attenuated the observed LEA. We assessed the overall LEA with all ceiling-performances removed and found a significant effect, $t(23) = -2.183$, $p = .04$, (*M* = -.734, *SD* = 1.648). A one-sample *t*-test examining overall accuracy revealed that performance on the task was above chance levels, $t(50) = 34.926$, $p < .001$ (chance = .08, *M* = .888 *SD* = .165).

2.2.3 Lateral Preferences

Participants were all right-handed (*M* = 21.53, *SD* = 4.33). Forty-nine participants showed a right-foot preference, the remaining two participants showed no foot preference (*M* = 5.31, *SD* = 2.33). Handedness and footedness were significantly correlated ($r = .436$, $p = .001$). Neither handedness nor footedness varied significantly with performance on the FWRT (Hand: $r = .106$, $p = .46$; Foot: $r = -.156$, $p = .274$). Similarly, neither handedness nor footedness varied significantly with performance on the EST (Hand: $r = .045$, $p = .752$; Foot: $r = -.023$, $p = .873$).

2.2.4 Complementarity of Speech and Emotional Vocalization Processing

The correlation between FRWT and EST lambda scores was not significant, $r = .101$, $p = .482$ (See Figure 2.1). Most participants displayed the typical complementary pattern of left-hemispheric dominance for speech processing and right-hemispheric

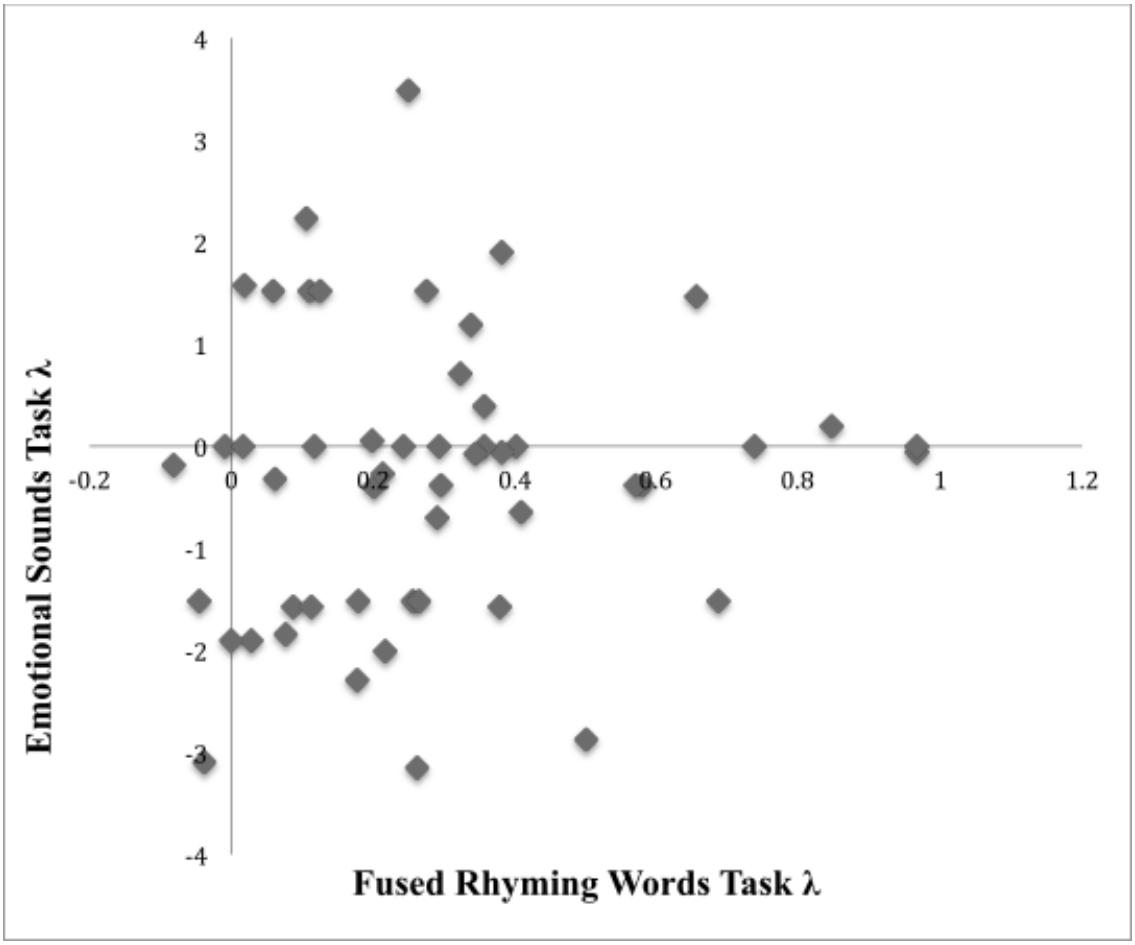

Figure 2.1. Individual λ scores on the Fused Rhyming Words Test (FRWT) versus λ scores on the Emotional Sounds Task (EST) for all participants. Positive values indicate a right ear advantage (REA).

dominance for emotional vocalization processing (29/52 = 57%), and only one participant showed the reverse pattern of hemispheric dominance (1/51 = 2%). The remaining participants demonstrated same-side dominance for both tasks, with 18/51 (35%) of participants displaying left-hemisphere dominance and 3/51 (6%) of participants displaying right-hemisphere dominance. As the presence of ceiling performances may have influenced the overall pattern of results, we also examined the correlation between

FRWT and EST lambda scores with all ceiling performances removed. The correlation was not significant, $r = .247$, $p = .245$ (see Figure 2.2). The majority of participants

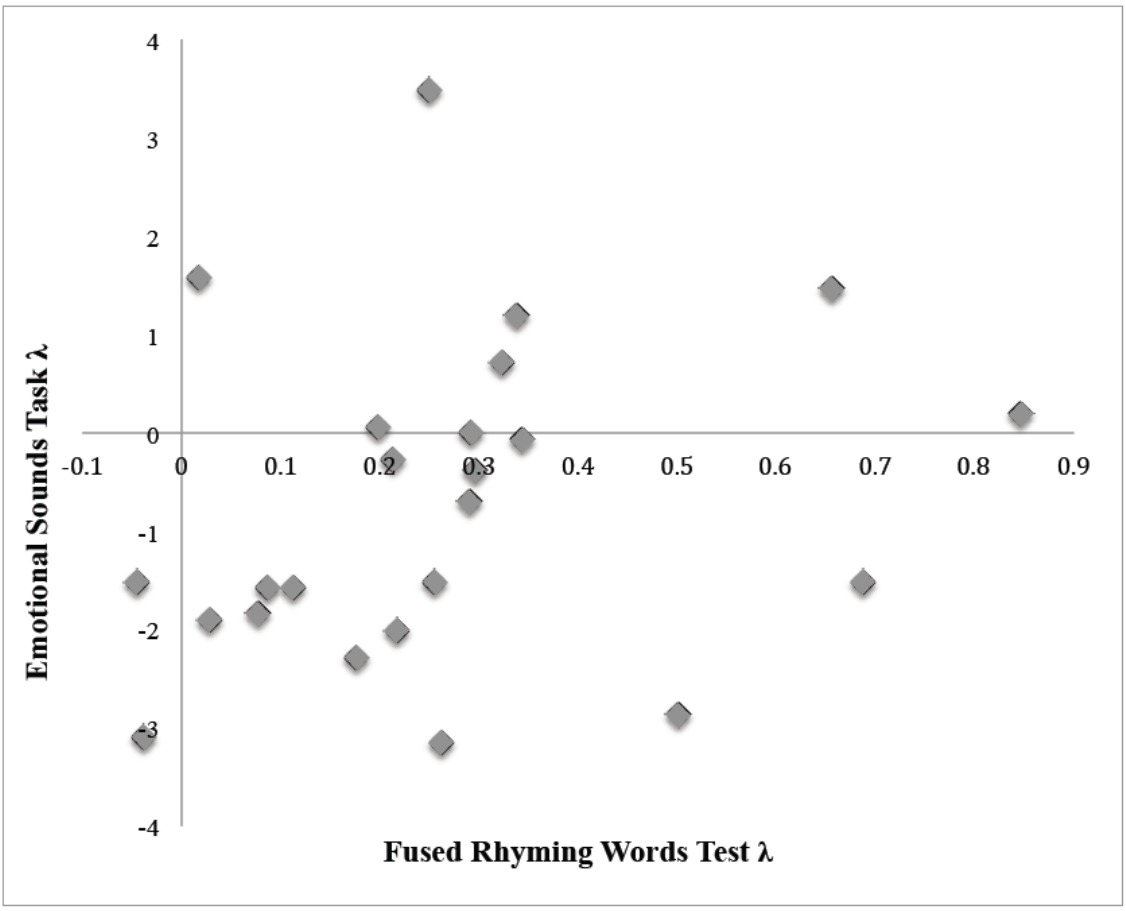

Figure 2.2. Individual λ scores on the Fused Rhyming Words Test (FRWT) versus λ scores on the Emotional Sounds Task (EST) with participants performing at ceiling on the EST removed. Positive values indicate a right ear advantage (REA).

displayed left-hemisphere dominance for speech processing and right-hemisphere dominance for emotional vocalization processing (15/24 = 63%), and no participants displayed the reverse pattern of hemispheric dominance. Again, the remaining participants demonstrated same-side dominance for both tasks, with 7/24 (29%) of

participants displaying left-hemisphere dominance and 2/24 (8%) of participants displaying right-hemisphere dominance.

2.3 Discussion

This present study examined the pattern of asymmetrical lateralization observed between speech vocalization processing within individuals, using the FRWT (Wexler & Halwes, 1983), and paralinguistic emotional vocalization processing, using an emotional sounds task (EST). Of the few studies examining the within-subjects pattern of lateralization using a variety of cognitive processing tasks, most have provided additional evidence for a statistical pattern of complementarity between right- and left-lateralized functions (Hellige, Bloch, & Taylor, 1988; Nestor & Safer, 1990). For example, Andresen and Marsolek (2005) examined lateralization of shape-recognition and spatial-relations within individuals and found no significant correlations between these, respectively, left- and right-lateralized tasks, suggesting a statistical pattern of lateralization between the tasks. Examining the more broad relationship between right- and left-lateralized cognitive functions, there have also been a few studies that have found evidence of either bias (Elias, Bulman-Fleming, and Guylee, 1999; Whitehouse and Bishop, 2009) or causal (Badzakova-Trajkov, Haberling, Roberts, & Corballis, 2010) patterns of lateralization.

As highlighted by Andresen and Marsolek (2005), a statistical pattern of complementarity need not predict only null correlations. In its strictest version, statistical complementarity may predict that all cognitive functions are lateralized by independent sources; however, a less strict view of the statistical pattern would predict a finite number of independent sources underlying the lateralization of cognitive functions. Under this

view, it is not unexpected, then, that a single source may influence asymmetrical lateralization of more than one function. This would result in a mixed pattern of results overall whereby some functions show independent (statistical) relationships with one another and causal or bias relationships with other functions. The fairly consistent finding of a statistical pattern across the literature (Andresen & Marsolek, 2005; Hellige, Bloch, & Taylor, 1988; Ley & Bryden, 1982; McNeely & Parlow, 2001; Nestor & Safer, 1990; Saxby & Bryden, 1984), punctuated by a few significant positive (Elias, Bulman-Fleming, & Guylee, 1999) or negative (Badzakova-Trajkov, et al., 2010) correlations between specific cognitive processes, may reflect a less strict form of statistical complementarity whereby lateralization for most cognitive functions is driven by independent processes, with a few processes lateralized by a common influence.

For this study, non-linguistic human emotional sounds were chosen to isolate the paralinguistic information from the influence of any linguistic processing. The stimuli were similar to those employed by King and Kimura (1972) and Carmon and Nachshon (1973), both of whom observed slight LEA for processing of these non-linguistic emotional sounds, but the method of responding differed. In our task we chose to have participants provide a present/absent response for their target emotion rather than reporting the two sounds heard following presentation of four binaural auditory choices (King and Kimura, 1972) or presentation of a visual selection display (Carmon and Nachshon, 1973). This method was chosen to reduce the potential for performance influence due to a high memory load (Bryden, 1982). These methodological differences did appear make the task too simple, as evidenced by the high proportion of participants achieving ceiling performance.

Analysis of the overall lateral biases for the speech and emotional vocalization processing tasks revealed a significant REA on the FRWT and a significant LEA on the EST, following removal of ceiling performances. These observed lateral biases replicated the expected population-level pattern of lateralization across the sample; however, further examination of the relationship between the degrees of lateralization on these two tasks within participants revealed a statistical pattern of complementarity suggesting the influence of independent processes on the lateralization of speech and emotional vocalization processing.

These results are consistent with the findings of McNeely and Parlow (2001) who examined the complementarity of linguistic and prosodic processing. They measured linguistic lateralization using the FRWT and measured prosodic lateralization using the Dichotic Emotion Recognition Test (DERT). In the DERT, pairs of nonsense sentences are presented dichotically, one in a neutral tone and the other in an emotional tone (happy, sad, angry, or afraid). Participants are asked to report the emotional tone for each pair presented. They observed an overall right ear advantage for linguistic processing and an overall left ear advantage for prosodic processing, but no significant correlation between the two functions was observed when assessed within individuals. Other studies examining lateralization of linguistic and prosodic processing have also reported similar findings: Ley and Bryden (1982) presented sentences spoken in emotional tones to participants and observed a similar population-level pattern with a REA for the linguistic content of the stimuli and a LEA for the emotional content; however, the overall pattern when examining performance within subjects reflected a statistical pattern. Using a similar method and procedure, Saxby and Bryden (1984) examined the lateralization or

emotional and linguistic processing in kindergarten, grade 4, and grade 8 children; no association between linguistic and emotional lateralization was observed, suggesting a statistical pattern of complementarity.

Our results are inconsistent with the findings of Elias, Bulman-Fleming, and Guylee (1999) who examined the relationship between lateralized linguistic and prosodic processing within individuals displaying atypical laterality profiles. They also measured linguistic lateralization using the FRWT. Prosodic lateralization was measured using the Emotional Words Task (EWT; Bryden & MacRae, 1989) where two-syllable, rhyming words, differing in the first phoneme (bower, dower, tower, and power) are presented in one of four emotional tones (happy, sad, angry, or neutral). A pair of words is presented, one word to each ear, and participants are asked to report which emotional tone they heard. Elias and colleagues found the expected population-level pattern of laterality for linguistic and prosodic processing across the sample, with an overall REA for the FRWT and an overall LEA for the EWT. In contrast to our findings, they observed a significant positive correlation between the tasks, suggesting a bias pattern of complementarity. The specific recruitment of participants with laterality profiles instead of relying solely on right-handers alone may explain the differences in findings between the two studies. For example, left-handers are much more likely to show right-hemisphere lateralization for language compared to right-handers. This increase in variability with regard to lateralization may influence the pattern observed.

2.4 Conclusion

An examination of the lateralization of speech and emotional vocalization processing revealed an expected overall complementary pattern of lateralization;

however, further examination of the relationship in degree and direction of lateralization between these two functions within individuals revealed evidence of a statistical pattern of complementarity. These present results provide additional evidence that the discrete asymmetries observed across individuals may not reflect the patterns and relationships observed when these asymmetries are examined together within individuals. Rather, these findings provide support for a statistical complementarity pattern reflecting independent processes governing the lateralization of linguistic and emotional processing.

3. Experiment 2: Melody and Language: An Examination of the Relationship Between Complementary Processes[2]

Music and language are both unique in that they are exclusive to human experience and they are both universally present in every culture (Nettl, 2000). In addition, both functions share common processing features – music and language both rely on the ability to process temporal auditory complexity, tonal structure at the global and local level, syntax, and sequence (Patel, 2008). Indeed, there is some strong evidence to suggest a large degree of overlap in the processing networks for music and language (Brown, Martinez, & Parsons, 2006; Levitin & Menon, 2003; Schön, Gordon, & Besson, 2005; but see Peretz & Zatorre, 2005). Finally, both functions are known to be highly lateralized, with specific features of music and language processing showing left or right hemisphere processing advantages (Bever & Chiarello, 1974). The degree of similarity in processing and evidence of a shared processing network hints at a common developmental origin underlying these two cognitive functions (Falk, 2000; Jerison, 2000; Finlay & Darlington, 1995). We cannot provide informative and effectively testable theories of developmental origin for these functions until we understand the relationship between them. This invites the question: do these two cognitive functions share a common lateralizing influence?

Music is multifaceted with both the left and right hemispheres playing active roles in the different aspects of musical-stimuli processing. The left hemisphere is involved in rhythm and temporal processing (Sakai et al., 1999), familiarity (Ayotte, Peretz,

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Rousseau, Bard, & Bojanowski, 2000; Platel, et al., 1997), and local interval processing (Peretz, 1990; Peretz, Morais, & Bertelson, 1987). The right hemisphere is known to be involved in contour processing (Liégeois-Chauvel, Peretz, Babai, Laguitton, & Chauvel, 1998), harmony (Koelsch, Gunter, Wittforth, & Sammier, 2005), and melody recognition (Kimura, 1964; Marin & Perry, 1999). Melodic processing is of particular interest as a melody has the ability to convey information in much the same way as language; a melody can convey meaning through syntactic structure, emotion, emphasis, and context by mirroring or contrasting a particular theme or feel in tempo, pitch pattern, and dynamics (Patel, 2008).

Evidence for right-hemisphere dominance in melodic processing comes from three key sources: first, work focused on patient populations with unilateral lesions or lobectomies has revealed a consistent pattern of melodic recognition deficit following right-hemisphere damage (Ayotte, et al., 2000; Milner, 1962; Samson & Zatorre, 1988; 1991). Steinke, Cuddy, and Jakobson (2001) examined melody recognition in a stroke patient (KB) with right-hemisphere damage. KB demonstrated significant impairment in familiar melody recognition for instrumental melodies. Interestingly, KB was still able to recognize familiar song (lyrical) melodies even when the melodies were played without the lyrics.

A second source of evidence for right-hemisphere dominance in melody recognition comes from dichotic-listening studies in neurologically healthy populations (Kimura, 1964; Messerli, Pegna, & Sordet, 1995; Zatorre, 1979). Boucher and Bryden (1997) used one-second, single-instrument melodies excerpted from classical works, which they played at a speeded rate of 400 bps. They presented dichotic pairs of the

melodies and asked participants listen for a specific target melody. An overall left ear advantage (LEA) for melody recognition was observed.

The third source of evidence for right-hemisphere dominance in melody recognition comes from neuroimaging work in neurologically healthy populations (Peretz, et al., 2009; Platel, Baron, Desgranges, Bernard, & Eustache, 2003). Patterson, Uppenkamp, Johnsrude, and Griffiths (2002) found greater right-hemisphere activation in the temporal region using fMRI in response to melodic stimuli compared to fixed-pitch stimuli. Additional work by Platel et al. (1997) examined the influence of familiarity on melody recognition and found right-hemisphere dominance when the melodies were unfamiliar but found more bilateral activation when melodies were familiar to the participants. Taken together, there is clear evidence for a dominant role of the right hemisphere in processing melodic information.

Language, much like music, is also multifaceted, and involves both left and right hemisphere processes. The right hemisphere is shown to be involved in processing the paralinguistic features of language such as prosody (Belin, Zatorre, & Ahad, 2002; Grimshaw, 1998; Ley & Bryden, 1982; Poeppel, 2003; for a review see Lindell, 2006), but it is the left hemisphere's dominance for processing semantic meaning, syntax, and phonology that is the hallmark of language lateralization (Broca, 1861; Frederici & Alter, 2004; Geschwind, 1979; Hecaen, DeAgostini, & Monzon-Montes, 1981; Kimura, 1961).

This population-level pattern of lateralization for linguistic and melodic processing is consistent with Bryden's (1990) Modal Model of cerebral organization, which proposes a differentiation of processing abilities between the two hemispheres (Corballis, 1991; Sperry, 1982) resulting in more efficient cognitive processing

(Bradshaw 2001; Levy, 1977). According to this view, the right hemisphere is specialized for holistic, integrative processing of information whereas the left hemisphere is specialized for serial, sequential, and analytic processing of information (Hellige, 1993). This complementary organization of left- and right-lateralized functions is often taken as evidence for the Modal Model; however, an examination of the correlation of the degree of lateralization between these functions within-subjects is necessary to establish whether or not a true relationship is present.

Three possible patterns of complementarity can be observed when examining the relationship between a left- and a right-lateralized cognitive process. The first pattern is causal complementarity (Bryden, 1990; Bryden, Hecaen, & DeAgostini, 1983). This pattern reflects a relationship where the asymmetrical lateralization of one cognitive function impels the opposite lateralization of the other function. For example, the specialization of the left hemisphere for linguistic processing leads to right-hemispheric lateralization for non-linguistic processes. As this pattern predicts opposite lateralization for complementary processes; in cases where language is found to be lateralized to the right hemisphere, this pattern would predict that non-linguistic processes would then be lateralized to the left-hemisphere. As such, a negative correlation in the degree of lateralization between the left- and right-hemisphere functions should be observed.

The second pattern is bias complementarity (Bryden, 1990). This pattern reflects the influence of asymmetries of either ascending sensory systems or attention, producing an overall bias for cognitive processing (Efron, Koss, & Yund, 1983; Kinsbourne, 1975; Sidtis, 1982; Teng, 1981). As the bias influences either a complete sensory system or a global attentional mechanism the bias complementarity pattern predicts that a strong right

ear advantage (REA) for a left hemisphere lateralized task will be accompanied by a weak REA for a right hemisphere lateralized task (and vice versa); thus, a positive correlation in the degree of lateralization between the two functions should be observed. Unlike the causal pattern, bias complementarity does not predict lateralization to opposite hemispheres for complementary processes.

The third pattern is statistical complementarity (Bryden 1982; Bryden 1990; Bryden, Hecaen, & DeAgostini, 1983). This pattern reflects independent sources influencing asymmetrical lateralization of cognitive processes. As such, each cognitive function carries a specific probability of being lateralized to either the right or left hemisphere depending on the source of influence. The two functions may be consistently lateralized to opposite hemispheres through separate, independent influences. A statistical pattern suggests that the population-level pattern of lateralization has been determined by chance and that the lateralization of one process to a particular hemisphere says nothing of the nature of the processes lateralized to the other hemisphere within an individual (Bryden, 1982). An examination of the relationship between two such statistically independent cognitive functions would reveal no correlation.

Few studies have directly examined the relationship in degree and direction of lateralization between left- and right-lateralized tasks within individuals. Ley and Bryden (1982) examined complementarity of linguistic and emotional processing using sentences spoken in emotional tones. They observed the expected population-level pattern with a REA observed for the linguistic content of the sentence stimuli and a LEA for the emotional content; however, when the relationship between the left- and right-lateralized tasks was examined, no significant correlation was observed. The authors argued that this

result provides support for the statistical model of complementarity. Using a similar method, Saxby and Bryden (1984) assessed the lateralization of emotional and linguistic processing in kindergarten, grade 4, and grade 8 children; they found no predictive relationship in the degree of lateralization for linguistic and emotional processing, again suggesting a statistical pattern of complementarity. Finally, similar evidence in support of statistical complementarity was found by McNeely and Parlow (2001) who also examined the complementarity of linguistic and prosodic processing. They measured linguistic lateralization using the Fused Words Dichotic-listening Task (FWDT) and measured prosodic lateralization using the Dichotic Emotion Recognition Test (DERT). The expected population-level pattern was observed: an overall REA for linguistic processing and an overall LEA for prosodic processing, but no significant correlation between the two functions was observed when the relationship was examined within individuals.

Similar evidence in support of statistical complementarity has come from recent studies using functional transcranial Doppler (fTCD) to measure lateral differences in cerebral blood flow. Whitehouse and Bishop (2009) examined the relationship between fTCD laterality indices (LI) for both visuospatial memory and lingusitic processing. They found no significant relationship between the two complementary functions. Similarly, Rosch, Bishop, and Badcock (2012) found no significant correlation between fTCD laterality indices measured during word generation and those measured during a visuospatial landmark task.

Not all research in this area has found evidence consistent with a statistical pattern of complementarity. To the best of our knowledge, two studies have found evidence

against a statistical pattern of complementarity. Elias, Bulman-Fleming, and Guylee (1999) examined the relationship between lateralized linguistic and prosodic processing within individuals displaying atypical laterality profiles. Elias and colleagues found the expected population-level pattern of laterality for linguistic and prosodic processing across the sample, with an overall REA for the linguistic processing task and an overall LEA for the prosodic processing task. In contrast to the previous findings, they observed a significant positive correlation between the two lateralized tasks suggesting a bias pattern of complementarity. The other discrepant finding in this body of research comes from a functional magnetic resonance imaging (fMRI) study examining the lateralization of face, linguistic, and visuospatial processing. Badzakova-Trajkov, Haberling, Roberts, and Corballis (2010) found partial support for causal complementarity with significant negative correlations observed between LIs recorded during word generation and LIs recorded during both an emotional facial processing task and a visuospatial landmark task. An additional non-significant positive correlation was observed between the LIs for emotional face processing and visuospatial processing. The authors argued that these results suggest the influence of multiple lateralizing influences.

Despite the evidence in support of a left-hemisphere dominance for linguistic processing and a right-hemisphere dominance for melody recognition, the issue of complementarity has not been researched within-subjects using music processing tasks; more specifically, the relationship between melodic and linguistic processing has not yet been examined. Do these population-level biases reflect a true causal pattern at the level of the individual? The present study examined both the global, population-level pattern of lateralization for linguistic and melodic processing as well as relationship between the

degrees and direction of lateralization observed for the two cognitive processes at the individual level using dichotic-listening tasks. The three patterns of complementarity provide three possible outcomes of this examination: first, if a causal relationship exists between linguistic and melodic recognition, then a significant negative correlation between laterality scores for the two tasks should be observed, indicating clear opposite lateralization. Second, if the lateralization of these two cognitive processes is governed by an attentional or sensory system bias, then a significant positive correlation should be observed, indicating a greater bias for one hemisphere or the other overall. Third, if the mechanisms directing lateralization of these two processes are independent of one another then no significant correlation should be observed, indicating no relationship between the lateralized tasks.

3.1 Method

3.1.1 Participants

Participants in the present study were 49 (9 male and 40 female) undergraduate students from the University of Saskatchewan who participated for course credit (mean age = 19.4, *SD* = 1.94). All participants were right handed (mean score 22.35, SD = 4.43); handedness was assessed using the Waterloo Handedness Questionnaire (see Elias, Bryden, & Bulman-Fleming, 1998). Right-handed participants were exclusively recruited for this study as they show a greater consistency in the lateralization of cognitive functions as compared to left-handers or mixed-handers (Bryden, 1982; Hellige, 1993). Additionally, only participants without formal music training or education were recruited. All participants in the study reported normal hearing with no history of hearing loss. The data from one participant was excluded because of a failure to follow task instructions.

All participants gave written consent prior to completing the experiment, and the procedures used received approval from the Ethics Review Board of the University of Saskatchewan.

3.1.2 Materials

3.1.2.1 Fused Dichotic Words Test (FDWT).

Participants' language lateralization was assessed using the Fused Dichotic Words Test (FDWT; Wexler & Halwes, 1983). Fifteen pairs of rhymed words are presented dichotically; the rhymed words differ only on the initial phoneme sound (e.g. deer and tear). The two words fuse when presented simultaneously resulting in the perception of a single word. The rhyming word stimuli were played on CD via Windows Media Player through Sennheiser headphones (model HD-437). The rhyming word pairs were presented 16 times (eight times on each channel) for a total of 240 trials. These trials were presented in two main blocks of 120 trials each (Block A and Block B). Each of these main blocks was further divided into four blocks of 30 trials each for a total of eight blocks. Participants were asked to circle which word was heard from a list of four possible choices in the provided answer booklet.

3.1.2.2 Unfamiliar Melody Recognition Task (UMRT).

An unfamiliar melody recognition task was developed for the present study to assess lateralization for melodic processing. Kimura (1964) found a significant left ear advantage for melody recognition using samples of orchestral music that differed in rhythm, timbre, and tempo. Similarly, Messerli, et al. (1995) and Boucher and Bryden (1997) also found overall LEAs when presenting single-instrument melodies differing in rhythm to non-musicians. As melody is typically defined as a sequential series of pitches

(Patel, 2008) and is argued to be distinct from other musical elements such as rhythm and timbre (Limb, 2006), we based our task on these previous studies but simplified the stimuli, holding rhythm, timbre, and tempo constant across the melodies, altering only the pattern of pitches presented. This approach allows us to assess the lateralization of melodic pitch-sequence processing in isolation.

A stimulus set of 12 monodic melodies was created using an M-Audio Keystation Pro 88 synthesizer and Finale Allegro composition software. The stimulus melody files were produced with a sampling rate of 44.1 KHz at a resolution of 16 bits. Each melody was seven quarter notes in length and was generated using the grand piano sound. All melodies were played in the C major scale, beginning on middle C (261.6 Hz) and ending on the tonic - either C4 (261.1 Hz) or C5 (523.3 Hz). The note values of the melodies ranged from an octave below middle C (C3: 130.8 Hz) to an octave above middle C (C5: 523.3 Hz). Each melody was 1000ms in duration, played at 240 bpm; all melodies were equalized for intensity. Each of the 12 melodies was paired dichotically with every other melody to create a total of 132 melody pairs. The melodies were presented using E-prime (Psychology Software Tools).

3.1.3 Procedure

Participants were tested individually. Following provision of informed consent, the participants were asked to fill out a demographics questionnaire (see Elias, Bryden, & Bulman-Fleming, 1998) assessing handedness, footedness, sex, age, and the presence of vision or hearing impairments. A second questionnaire assessed musical experience. Participants then completed the FDWT and the UMRT; order of presentation of the two

tasks was counterbalanced across participants. All tasks were completed in a single session approximately one hour in duration.

3.1.3.1 FDWT.

The participants were seated at a table and were given a set of headphones and a response booklet to report their responses during the task. Once the task instructions had been given the participants completed a set of 30 practice trials; these trials were single-word, binaural presentations of the 30 words used to create the rhymed pairs. Participants were asked to circle which word they had heard presented in the response booklet. Following the test trials participants completed the eight blocks of test trials. The rhyming word pairs were presented with an interstimulus interval of 2.5 seconds. Participants were given a brief rest period following each block of trials; headphone position was reversed after blocks 1, 3, 5, and 7 to control for channel effects.

3.1.3.2 UMRT.

The participants were seated in front of a computer monitor and keyboard; they were first presented with a target melody. The melody was played five times to familiarize the participant with their specific target; the participant initiated each presentation of the target melody with a key press. Participants then completed a set of 26 practice trials. Participants were instructed to place their index and middle fingers of their right hand on the ’y’ and ‘u’ keys, respectively. A single melody was presented binaurally following which the participant was prompted to indicate whether their target melody had been played by pressing the yes key (y) or the no key (u) on the keyboard. During sound presentation the monitor displayed a black screen; following completion of the melody presentation a response prompt was presented on the screen (“yes or no?”). The

participant's response on a given trial triggered the start of the next trial. Once the practice trials were completed, the participants were prompted to press the space bar to begin the test trials.

The test trials followed the same procedure as the practice trials except a dichotic melody pair was presented in place of the binaurally presented single melody. Participants were again prompted to indicate whether their target melody was presented in either ear by pressing the yes or no key following each dichotic melody pair presentation. After completing the first block of 132 test trials, participants were assigned a new target melody, the headphones were reversed, and the task was repeated. Participants each completed two blocks of trials in total. Order of target melodies was pseudo-randomized and counterbalanced across participants.

3.1.3.3 Calculation of asymmetry scores

Lambda (λ) scores were calculated for FDWT and UMRT data (see Bryden and Sprott, 1981):

$$= \ln\left(\frac{(\text{REcorrect} + .005)(\text{LEincorrect} + .005)}{(\text{LEcorrect} + .005)(\text{REincorrect} + .005)}\right)$$

RE indicates right ear responses and LE indicates left ear responses. The addition of a constant value (.005) allowed for calculations if one or more of the observed values were equal to zero. This calculation provides a measure of laterality that is based on the log-odds ratio. This measure is approximately normally distributed and is independent of overall performance on the tasks. Positive λ values reflect a right-ear performance advantage (REA) indicative of a left-hemisphere processing advantage.

3.2 Results

3.2.1 FDWT

To assess the potential influence of block order, performance on block A and block B of the task was compared; no difference was observed, $t(47) = -.416$, $p = .679$. All data was collapsed for the remaining analyses. A right ear advantage (REA) was observed for 98% (47/48) of participants for the FWDT. The overall REA for the task was significant, $t(47) = 8.896$, $p < .001$ ($M = .317$, $SD = .247$). An analysis of overall accuracy revealed above-chance performance on the FDWT, $t(47) = 85.382$, $p < .001$ (chance = 120 correct responses (50%), $M = 229.396$, $SD = 8.878$). See Table 1 for mean performance by ear.

Table 3.1. *Mean performance percentages*

Task	Left Ear	Right Ear
FDWT	40.4	55.2
UMRT	49.9	52.7

3.2.2 UMRT

To assess a potential influence of target melody, a one-way ANOVA compared performance across all melodies; no significant difference was found, $F(12, 96) = 1.122$, $p = .355$. A 2 x 2 repeated measures ANOVA assessed the effects of testing block order (first and second) and ear (left and right) using percent correct performance values. The main effect of block was not significant, $F(1, 47) = .633$, $p = .430$. Similarly, no main effect of ear was observed, $F(1, 47) = 1.691$, $p = .200$. The interaction between block and

ear was also not significant, $F(1, 47) = 1.140$, $p = .291$. As no significant differences between the test blocks were observed, the data were collapsed for subsequent analyses. A LEA was observed for 35% (17/48) of participants. Two participants did not elicit an ear advantage on the task; one participant was added to the REA group and the other to the LEA group for subsequent analyses. A one-sample *t*-test using the λ scores as a measure of overall ear advantage for the UMRT revealed no significant ear advantage, $t(47) = 1.488$, $p = .143$ ($M = .271$, $SD = 1.261$). A one-sample t-test to assess accuracy on the task revealed that performance was above chance levels $t(47) = 15.915$, $p < .001$ (Chance = 8% (11 correct yes responses) $M = 51.29$, $SD = 18.8$). Assuming an equal distribution of yes and no responses, approximately half of all target-present trials would receive correct responses at chance performance. Chance performance on the task is calculated at 8% as only 16% of trials are target-present trials.

3.2.3 Lateral Preferences

All participants were right-handed ($M = 22.35$, $SD = 4.43$). Forty-five participants showed a right-foot preference, two participants showed a left-foot preference, and one participant failed to show a preference for either foot ($M = 5.45$, $SD = 3.33$). Handedness and footedness were found to be positively correlated, $r = .385$, $p = .007$. There were no significant correlations observed between performance on the FDWT and degree of handedness ($r = .147$, $p = .318$) or footedness ($r = .016$, $p = .912$). Significant positive correlations were observed between performance on the UMRT and degree of handedness ($r = .396$, $p = .005$) as well as degree of footedness ($r = .294$, $p = .043$) indicating that more strongly right-handed and right-footed participants show greater REAs (left-hemisphere lateralization) on the melody task.

3.2.4 Correlation Between Linguistic and Melodic Processing

We assessed the relationship between linguistic and melodic lateralization; the complementary pattern of left-hemisphere dominance (REA) for the linguistic task and right-hemisphere dominance (LEA) for the melodic recognition task was observed in 38% (18/48) of participants. The reverse pattern of lateralization was only observed in one participant (1/48 = 2%). Most participants displayed left-hemisphere dominance for both the linguistic and melodic recognition tasks (29/48 = 60%). No participants displayed right-hemisphere same-side dominance for both tasks. A non-significant positive correlation between the FDWT and UMRT λ scores was observed, $r = .259$, $p = .076$ (See Figure 3.1).

3.2.5 Influence of Musical Experience

To assess the possible influence of musical experience on melody recognition performance (operationalized as the number of hours spent listening to music per week), we performed a regression analysis using the overall task accuracy as the independent variable and the number of hours spent listening to music per week as the dependent variable. There was no significant relationship between musical experience and overall UMRT task accuracy observed ($r = .107$, $b = .003$, $p = .474$). This suggests that participants who spend more time listening to music do not tend to show greater accuracy on the UMRT than those participants who do not listen to music as frequently. Similarly, we assessed the relationship between the observed λ values for the UMRT task and musical experience. Again, no significant relationship was observed ($r = .016$, $b = .003$, $p = .915$). This result suggests that participants who listen to music more frequently are not more likely to show greater bias scores (ear-advantages) on the UMRT.

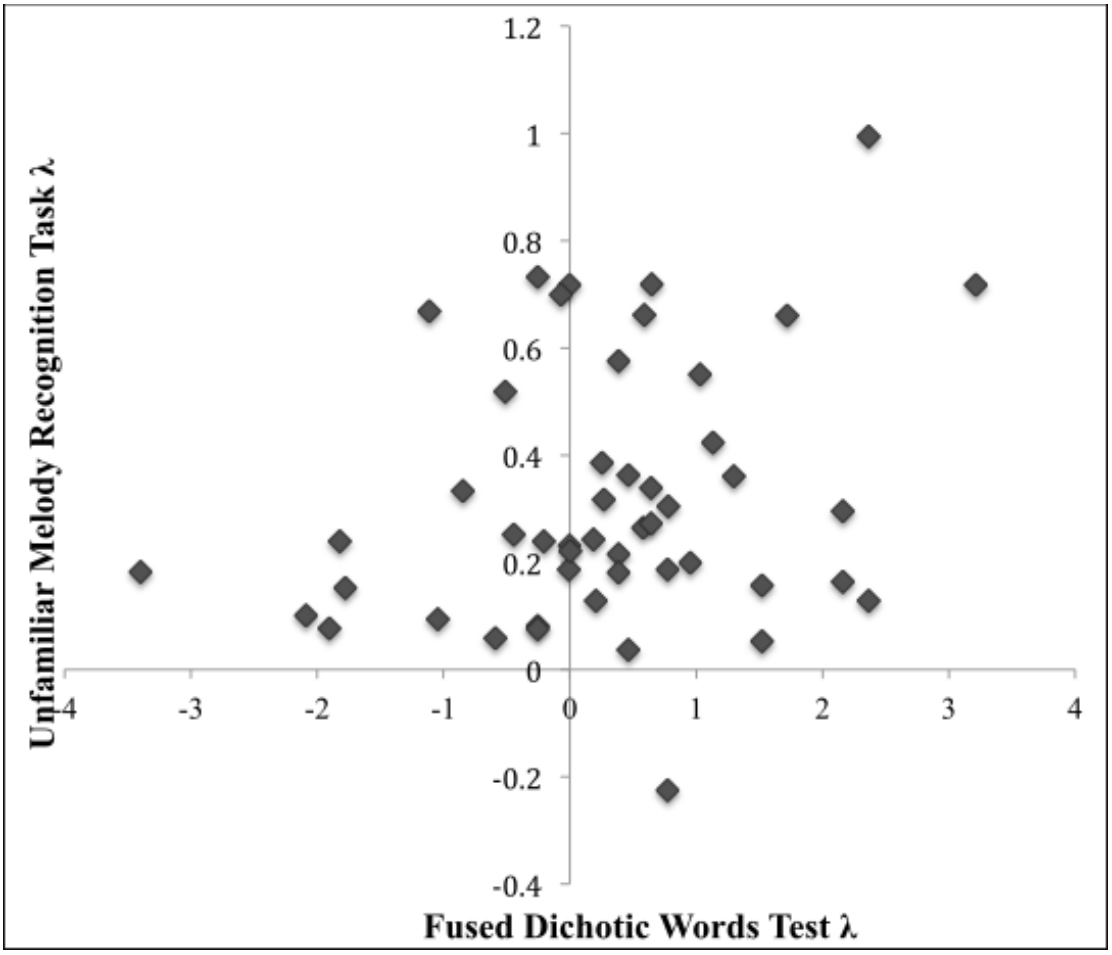

Figure 3.1. Individual λ scores on the Fused Dichotic Words Test (FDWT) versus λ scores on the Unfamiliar Melody Recognition Task (UMRT) for all participants. Positive values indicate a right ear advantage (REA).

3.3 Discussion

We examined the pattern of complementarity observed between linguistic processing (FDWT) and unfamiliar melody recognition (UMRT). We observed the expected REA in the linguistic task, but failed to observe a significant LEA for unfamiliar melody recognition. The number of hours spent listening to music did not

influence either performance or degree of lateralization on the melody recognition task. Handedness and footedness were both found to be positively correlated with degree of lateralization for melody recognition. Finally, no relationship was observed between degree of laterality for the linguistic and melodic recognition tasks.

The overall REA observed for the linguistic processing task is consistent with the previous findings of a left-hemisphere dominance for language (Kimura, 1961; Ley & Bryden, 1982). The failure to find a significant LEA for the melody recognition task was unexpected, but can be explained by a shift in processing strategy for the task. Despite the evidence from studies demonstrating that melody recognition is more efficient when pitch information is presented in isolation from rhythm information (Hebert & Peretz, 1997; White, 1960), there is evidence suggesting that melodic processing is inherently rhythmical (Jones & Boltz, 1989). Kidd, Boltz, and Jones (1984) found that melodies with different pitch sequences were judged as being the same when they shared the same rhythmic structure. This suggests that both pitch and rhythm information may be perceived and processed as a single dimension in melody recognition. In fact, responses from participants following task completion in the present study frequently indicated that they did not hear the melody tokens as true melodies, rather they were perceived as a non-unified string of notes. The absence of rhythmic variation was often cited as the cause of this perception.

The similarity of rhythm across all the tokens in the UMRT, in addition to the limited pitch range and the similar starting note across tokens, may have biased participants to view the melodies as highly similar. Together these conditions may have resulted in participants switching from a global, contour-based strategy for melodic

processing to a more local, interval-based strategy. There is evidence to suggest that interval and contour information are processed with opposite hemispheres (left and right, respectively; Peretz et al., 1987; Peretz & Babai, 1992; Lee, Janata, Frost, Hanke, & Granger, 2011; but see Stewart, Overath, Warren, Foxton, & Griffiths, 2008). Peretz et al. (1987) demonstrated that a shift from a contour-based holistic processing strategy (LEA) to an interval-based analytic (REA) strategy could be induced by prompting participants to focus on specific notes or intervals within a presented melody. Such a shift in processing would result in increased reliance on left-hemisphere analytic processes, thus potentially explaining our failure to find a LEA for the UMRT.

A non-significant positive correlation between the λ values for the FDWT and the UMRT was observed. The failure to find a significant negative relationship suggests that participants showing a REA for the linguistic task are not more likely to show an LEA on the melody recognition task, as would be predicted by the Modal Model. This finding is not surprising, given the failure to elicit the expected LEA with the melody recognition task. As such, the relationship between the linguistic and melodic task laterality scores is not informative regarding the nature of complementary lateralization of the two functions; however, the positive direction of the correlation (approaching statistical significance), especially given the REA observed for both tasks, suggests the possibility of a shared processing network for the processing of linguistic and elements of musical stimuli.

Neuropsychological evidence for dissociation between the mechanisms governing music and language processing is compelling (Marin & Perry, 1999). For example, Peretz (1993) provided a description of patient G.L. who, following bilateral temporal lobe

damage, demonstrated a significant impairment in pitch tone interpretation in the absence of language processing difficulties. Conversely, Poeppel (2001) presents a case where bilateral temporal lobe damage resulted in total impairment in understanding spoken language while preserving the ability to process and identify musical or other environmental sounds. In contrast, neuroimaging studies have provided evidence suggesting that significant overlap exists in the processing networks for music and language (Hickock, Buchsbaum, Humphries, & Muftuler, 2003; Levitin, & Menon, 2003). For example, Brown, Martinez, and Parsons (2006) had participants complete sentence and melody fragments with spontaneous, improvised responses. Using positron emission tomography (PET), the authors found bilateral activation in superior temporal and inferior frontal regions for both the music and language generation tasks. In fact, the real difference between music and language processing did not seem to lie in the processing locations, rather more in the lateralization of the functions, with greater left hemisphere activation observed for language processing. They argued that these results provide evidence for a shared role in the generation of complex sounds.

Zatorre and Belin (2001) suggest that the left and right hemispheres are not specialized for language and music, respectively, but rather are specialized for specific aspects of sound processing, with the left hemisphere specialized for rapid temporal processing and the right hemisphere specialized for general pitch processing. According to this view, it is possible that participants resorting to an interval processing approach to the melody recognition task may have engaged left-hemisphere temporal processing mechanisms to process the temporal order of the relative pitches in the presented melodies. The observed positive correlation between the linguistic and melodic

processing tasks in our study may indicate a shared processing mechanism, as effective processing of linguistic stimuli requires rapid temporal sequencing.

Alternatively, Patel (2003) argues that music and language each have a domain-specific representational network where the knowledge systems for the two processes are thought to be independent (Fedorenko, Patel, Casasanto, Winawer, & Gibson, 2009). This can be thought of as a rule-book for the syntax and structural rules governing language and music composition. Patel also suggests that music and language each have a resource network used in the processing and integration of information during processing, and that these networks overlap resulting in shared processing. In essence, the resource networks are a sorting and organizing system allowing for rapid selection and associative activation of information during online processing. According to this view, it is possible that both the linguistic and melody recognition tasks in our study showed similar reliance on these shared resources for the rapid sequencing and processing of the structural information of both the words and melodies presented. To differentiate between these two potential explanations, further research is needed.

As our ability to examine the relationship between lateralization of linguistic and melodic processing was precluded by the failure to elicit the expected LEA for melodic processing. Additional examination of this relationship is needed, using tasks that more accurately capture the typical population-level pattern of lateralization. Further study of the relationship between left-lateralized linguistic processing and right-lateralized melodic processing would benefit from focusing more specifically on melodic contour information or including temporal information in the melodies presented in an attempt to reduce reliance on left-hemisphere processing strategies.

4. From Mechanisms to Consequences

To assess what pattern of complementary relationship exists between left- and right-lateralized functions in the brain, the pattern in the degree and direction of lateralization observed language processing and emotional (Experiment 1) and melodic (Experiment 2) processing were compared within individuals. Experiment 1 revealed the expected population-level asymmetries in task performance, but demonstrated statistical independence when compared within individuals rather than revealing the negative correlation predicted by the causal complementarity assumption inherent in many evolutionary theories of laterality. As the expected population-level asymmetry for melodic processing was not found for the right-hemisphere task in Experiment 2, an assessment of the complementary relationship between melodic and linguistic processing could not be made.

Together with the growing literature examining the issue of complementarity of cognitive processing, the results from Experiment 1 provide evidence in support of statistical complementarity between left- and right-hemisphere functions, suggesting that separate, independent forces lateralized the two functions. This finding highlights the need for an evolutionary theory of lateralization that takes into account the overall pattern of relationship between all left- and right-hemisphere functions rather than relying on an assumed causal relationship between two specific lateralized tasks such as language and visuospatial processing.

Accounting for the complex relationships between multiple functions, such a theory will lead to a greater understanding of the mechanisms that gave rise to these lateralized patterns of processing, but that still only addresses half of the story of

laterality. Evolutionary theories attempt to explain the causes of laterality, but they do not address the effects of laterality. The emergence of asymmetrically lateralized patterns of processing is likely to have consequences for the behaviours that are controlled by these processes. To fully understand the phenomenon of human cerebral lateralization, we must also examine what influences lateral biases in cognitive processing have on our everyday behaviours.

Evolutionary theories of laterality share the assumption of an adaptive advantage to functional lateralization of cognitive processing. Direct evidence of the influence of functional lateralization on behaviour can be easily observed in some cases, such as handedness. Here, the left hemisphere specialization for exerting precise control over complex sequences of action is thought to have resulted in an asymmetry favouring the right hand for fine motor tasks in the majority of individuals. The influence of cerebral lateralization of processing on other behaviours is less obvious. There are clear influences on task performance related to hemispheric lateralization of cognitive processes, such as ear advantages in word identification tasks; however, few studies have examined how these hemispheric processing asymmetries affect everyday behaviours beyond handedness.

5. Experiments 3 & 4: Put Your Best Side Forward: The Effect of Facial Attractiveness Asymmetry on Posing Biases

From 14th century paintings to modern photographs, there is a consistent bias for the subject of the portrait to be positioned so that the left cheek is displayed more prominently (McManus & Humphrey, 1973; Labar, 1973; Zaidel & Fitzgerald, 1994; Conesa, Brunold-Conesa, & Miron, 1995; Nicholls, Clode, Wood, & Wood, 1999; See Powell & Shirillo, 2009 for a review). In an examination of more than 1400 Western European paintings, McManus and Humphrey (1973) found that the subjects of painted portraits tended to display a left-cheek pose, with female portraits showing a greater leftward bias (68%) than male portraits (56%). This leftward bias in artwork portraiture was later confirmed by Conesa and colleagues (1995) in an examination of more than 4100 portrait paintings, etchings, drawings, and photographs. The posing bias is not limited to artwork. LaBar (1973) found a leftward posing bias in yearbook portraits, Bruno and Bertamini (2013) found a leftward posing bias in selfie portraits taken with a smartphone, and Thomas, Burkitt, and Saucier (2006) found a leftward posing bias in online photos of infants and non-human animals.

Explanations accounting for this bias are as varied as the studies that have demonstrated its presence across the genres of portraiture. One explanation rests on the dominant hand of the artist; handedness imposes certain mechanical restraints in the direction of the motions used to produce paint strokes or drawn lines. Right-handed artists, for example, may prefer to paint or draw left profiles as the subject placement allows them to use more abductive movements, or movements which follow the natural arc of the arm, to create the detailed features of the face in a profile portrait (Bradshaw,

Bradshaw, & Nettleton, 1980; Nicholls, et al., 1999). Despite these arguments, mechanical biases fail to account for two important aspects of the posing bias: First, mechanical biases do not provide an explanation for the sex difference in portraiture. Second, they cannot explain why a posing bias is present for photographs where artist handedness has little influence in how a photograph is captured. Further, an examination of the portraits painted by two prolific left-handed artists revealed the same leftward posing bias observed among portraits painted by their right-handed contemporaries rather than the rightward bias predicted by the reversed mechanical constraints for the left-handed artist (Nicholls, et al., 1999).

A second explanation for the leftward posing bias calls on asymmetries in the perceiver's visual processing. When attending to visual space, people generally show a slight but consistent bias in attention to the left side of the visual field (Bowers & Heilman, 1980; Jewell & McCourt, 2000). Additionally, people demonstrate an overall advantage for processing faces in the left side of visual space (Levine, Banich, & Koch-Weser, 1988; Levy, Heller, Banich, & Burton, 1983). These leftward biases are thought to be driven by the right hemisphere's dominance for attention and face processing (Bryden, 1982; Levy, et al, 1983). Consistent with these biases, Freimuth and Wapner (1979) found that individuals viewing paintings showed a tendency to focus on the elements on the left side of the piece. In portraiture, left-cheek poses place the key facial features of the subject in the left visual field of the viewer; this position facilitates the processing of the face as the visual information is sent directly to the right hemisphere for processing. However, when viewers were asked to rate portraits presented in both their original and mirror-reversed orientations, the viewers ratings did not differ between the

two orientations (Schirillo, 2000; Zaidel & Fitzgerald, 1994). This pattern suggests that the visual field in which the facial features are presented is not what influences the viewer's perception of the portrait. Interestingly, raters did show a preference for left-cheek images over right-cheek images (regardless of image orientation), suggesting that image preference was influenced by facial physiognomy of the portrait subject.

This finding of a preference bias based on facial physiognomy of the individual portrayed in the portrait lays the foundation for a third explanation for the leftward posing bias: lateral asymmetry in facial expression. There is a substantial body of evidence demonstrating that the left side of the face is more emotionally expressive than the right side of the face (Borod, Kent, Koff, Martin, & Alpert, 1988; Campbell, 1978; Sackheim, Gur, & Saucy, 1978; Skinner & Mullen, 1991; See Powell and Shirillo, 2009 for a review). For example, Sackeheim et al. (1978) used photographs to create composite faces. The left side of one face was paired with a mirror-reversed copy of the same half to create a left-left composite face. The same procedure was used with the right side of the face to create a right-right composite face. When participants were presented with a pair of composites and asked to choose which face appeared more emotionally expressive, the left-left composite was chosen most often. This asymmetry in emotional expression likely reflects the right hemisphere's dominance for emotional expression as the right hemisphere controls movement in the lower left side of the face (Borod, Haywood, & Koff, 1997).

Nicholls et al, (1999) suggested that this asymmetry in emotional expressivity might explain the leftward posing bias in portraiture. The desire to either express or hide emotion may guide the artist or the person posing to turn the left or right cheek forward,

respectively. Additionally, this explanation accounts for the stronger leftward posing bias observed for females; females show a greater tendency to reveal the more emotive left cheek as females are more apt to show their emotions than males (Brody & Hall, 1993; Fischer, 1993).

To test this hypothesis, Nicholls et al. (1999) asked participants to pose for either a family portrait where they were instructed to express their love and affection for their family or for a scientific portrait where they were instructed to conceal emotion and appear stoic. The participants' posing direction was recorded and revealed the predicted leftward bias for the emotional family portrait and a rightward bias for the stoic scientific portrait; the authors concluded that, when posing for a portrait, we intuitively know which side of the face is more expressive and purposefully position the left cheek to either convey or hide emotion. Additional studies examining both historical portraits (ten Cate, 2002) and modern web-page photographs (Churches et al, 2012) of professors and academics have confirmed the rightward bias for scientific portraits. In further support of the emotional expressivity explanation of the leftward posing bias, Nicholls, Clode, Lindell, and Wood (2002) examined the relationship between emotional expressivity scale scores and posing direction. Supporting the sex difference in posing bias, females were found to be more emotionally expressive than males and showed a greater leftward posing bias. Additionally, a trend for leftward posers to report higher levels of emotional expressivity compared to rightward posers was also observed.

Like emotional expression, attractiveness also seems to be represented asymmetrically on the face. Studies examining overall appeal and attractiveness ratings of both photographs and portraits have found higher ratings of attractiveness for the right

side of the face compared to the left (Benjafield & Segalowitz, 1993; Zaidel, Chen, & German, 1995; Schirillo, 2000). Zaidel and Fitzgerald (1994), in an examination of the leftward posing bias, asked participants to rate their overall "liking" of painted portraits. Contrary to the leftward posing bias widely observed in portraiture, participants showed a greater overall liking for right-cheeked portraits compared to left-cheek portraits, with the highest preference ratings for right-cheeked portraits of females. In their second experiment participants were asked to rate the same portraits on the attractiveness of the subject. Right-cheeked portraits were found to be more attractive compared to left-cheeked portraits; specifically, right-cheeked portraits of females were rated as significantly more attractive than left-cheeked portraits of females. No difference was found between right- and left-cheeked male portraits. As the right-cheek preference was found regardless of whether the portrait was presented in its original orientation or left-right reversed orientation, the authors proposed that the attractiveness ratings were influenced by physiognomic asymmetries in the face, with the right hemiface being viewed as more attractive overall. To further examine this bias, Zaidel, et al. (1995) presented pairs of left-left and right-right composite faces to participants and asked them to select which face appeared more attractive. Consistent with the earlier findings, right-right composites of female faces were judged to be more attractive than left-left composites of female faces. No difference in attractiveness ratings was found between the composites for male faces.

Not all studies have shown this consistent bias. Blackburn and Schirillo (2012) examined ratings of aesthetic appeal and measured pupil dilation as an indicator of interest and found that left-cheeked images produced higher subjective ratings and

greater pupil diameter measurements, indicative of greater interest, compared to right-cheeked images. Additionally, Dunstan and Lindell (2012) created image pairs, a leftward pose and a rightward pose, and asked participants to select which image appeared either happier or more attractive. They found a rightward bias in attractiveness for female portraits, but only when the image was presented in its original orientation. When the mirror-reversed image was presented, a leftward bias was observed suggesting a visual field influence rather than a right hemiface asymmetry in attractiveness. Despite these contrary findings, the majority of studies examining attractiveness have found a rightward bias, particularly for female subjects.

Interestingly, the leftward posing bias so prevalent in portraiture runs counter to the rightward attractiveness asymmetry, suggesting either that factors besides attractiveness govern posing direction or that right-cheek poses are not more attractive. What happens when the purpose of the image is solely to showcase attractiveness? Nicholls et al. (1999) provided evidence of an intuitive awareness of the asymmetry in emotional expressivity and its ability to influence posing behaviour to either maximize or minimize the emotional information we convey. Do we also possess a similar intuitive awareness of the asymmetry in facial attractiveness?

5.1 Experiment 3

If we are intuitively aware of the rightward attractiveness asymmetry then we should see a rightward posing bias when the portrait conditions should emphasize attractiveness and beauty qualities of the portrait subject. Modeling headshots are portraits specifically designed to highlight the most attractive features of the model. The current study was designed to assess whether a rightward posing bias, emphasizing the

more attractive right hemiface, is observed for modeling headshot portraits. We predict that an overall rightward posing bias will be observed with a greater bias for female models than for male models.

5.1.1 Methods

A total of 493 modeling headshot images were found using a Google Images search for the terms "modeling headshot" or "modeling photography." To ensure that only professional modeling photographs were used, images were selected from sites that offered professional modeling photography, professional modeling agency websites, or sites that featured images with professional photography credits. All single-subject images where the model was the clear focus of the image were used. A research assistant naive to the hypotheses of the study completed data collection and measurement.

For each image, the following information was recorded: the image URL and date accessed, the model's sex, the amount of the model's body that was visible in the image (head only, head and shoulders, or full torso), and the posing bias of the subject. Posing bias was determined using a ruler to measure the distance from the outer canthus of the eye to the center of the nose. A difference score was calculated subtracting the left side measurement from the right side measurement, so that positive values indicated a right-side posing bias, and negative values indicated a left-side posing bias. If the difference between the left and right distances was less than 2 mm, the posing direction was scored as no bias. If the outer canthus of the eye was obscured, then the distance from the center of the nose to the edge of the face nearest the eye was used. If the image showed a full profile shot (only one eye present in the image) no measurement was taken, and the side

of the profile was coded as the posing direction. The resulting posing biases were coded as -1 for a leftward bias, 0 for no bias (central pose), and +1 for a rightward bias.

5.1.2 Results

A Chi-square analysis revealed a significant posing bias for the modeling images, with leftward poses (n = 217) appearing more frequently than rightward (n = 126) or central (n = 150) poses; χ^2 (2, N = 493) = 27.071, p < .001, φ = .234. A second analysis with central poses removed confirmed that leftward poses occurred significantly more frequently that rightward poses; χ^2 (1, N = 343) = 24.143, p < .001, φ = .265.

A univariate ANOVA was used to examine the potential influence of subject sex (male, female) and body visibility (head, head and shoulders, full torso) on posing direction. There was no difference in posing bias between males and females; F(1, 487) = 2.538, p = .112, partial η^2 = .005. Similarly, no influence of body visibility was found; F(2, 487) = .944, p = .390 partial η^2 = .004. The interaction between sex and body visibility was also not significant; F(2, 487) = .826, p = .439 partial η^2 = .003.

5.1.3 Discussion

Contrary to the rightward posing bias suggested by the rightward attractiveness bias in the literature, a significant leftward posing bias for modeling headshot portraits (44% of images) was observed, consistent with the bias consistently observed in the general posing literature. Central poses (30%) also outnumbered the rightward poses (26%). The gender bias typically observed in both posing and attractiveness rating studies was not observed here; however, as images of females outnumbered images of males nearly 5:1, a larger, more balanced sample of male images is needed to conclusively examine the influence of subject sex on posing bias in modeling headshots.

The leftward bias observed here suggests that asymmetry in facial attractiveness does not influence the posing direction for publication of modeling headshot images. One question remains unaddressed: is the leftward bias in portraiture the direct result of the posing preference of the portrait subject or is it the result of a selection bias by the image viewer? It might be that models posing for their headshots choose to preferentially expose their right cheek when posing, but other factors that govern aesthetic preferences, such as frame composition (Locher, Overbeeke, & Stappers, 2005) or directionality of the image (Friedrich, Harms, & Elias, 2014), may lead the model, the photographer, or the publisher of the image to select a left-cheek image instead.

5.2 Experiment 4

To investigate whether the observed posing bias is the result of actual posing behaviour or due to image selection preferences, we examined the posing direction chosen by individuals asked to pose for a portrait. Using the method and family portrait posing condition from Nicholls et al's (1999) portrait posing study, participants were asked to pose for either a family portrait or a Vogue magazine cover shoot. If we are intuitively aware of the inherent asymmetry in facial attractiveness, participants who pose for the Vogue magazine cover shoot should show a rightward posing bias, whereas participants who pose for the family portrait should show a leftward posing bias consistent with the emotional expressivity bias.

5.2.1 Methods

5.2.1.1 Participants.

Seventy-five (16 males and 59 females) undergraduate students from the University of Saskatchewan participated in the present study for course credit (mean age

19.99, Range = 18-46). Sixty-seven of the participants were right-handed, as assessed by the short version of the Waterloo Handedness Questionnaire—Revised (Elias, Bryden, & Bulman-Fleming, 1998; *mean* = 20.99, *SD* = 4.00). Eight participants were left-handed (*mean* = -13.75, *SD* = 5.90).

5.2.1.2 Procedure.

Closely based on Nicholls et al.'s (1999) procedure, participants were randomly assigned to one of two portrait conditions (family portrait or magazine cover portrait) and were assigned a script to read. Participants assigned to the family portrait condition were given the following script: "You have a close-knit family including your parents, siblings, partner and two small children. You are going overseas for a year and want to have a portrait taken as a gift to them. You are a warm-hearted and affectionate person. You love your family and want the portrait to remind your family of how much you love them. To achieve this, you put as much real emotion and passion into the portrait as you can" (Nicholls et al., 1999, p.1520).

Participants in the magazine cover portrait condition were given the following script: "You are a successful model and are one of the most recognizable faces in popular media. You are naturally attractive and are very confident about your good looks. You have been selected to appear on the cover of Vogue – a great honour as it is the top magazine in fashion. In order to prepare for this prestigious photo shoot you have been working hard to eat healthy and keep extra fit to ensure you are in peak physical form. When you pose for your cover portrait you want to show the world just how good looking you really are. To do this try to emphasize your most attractive features."

Participants were seating in a room lit with symmetrical overhead halogen lighting. The room was symmetrical with the exception of a single window located on the left side of the room. The window was covered with a black-out shade during data collection, and participants were seated with their backs to the window. A camera on a tripod was positioned 1.8 meters in front of the participant with the experimenter positioned centrally behind the camera. Once seated, the participant was asked to read the script he or she had been assigned; the participant was then given 30 seconds to consider a posing position based on the scenario information. At the end of the 30 seconds, the participant was asked to pose for a portrait with explicit instructions not to face the camera straight-on. The experimenter recorded the participant's posing direction (left cheek forward or right cheek forward). Finally, participants filled out a demographics questionnaire that assessed handedness and footedness (Elias et al., 1998), as well as participant sex and age. Once the questionnaire was completed, participants were debriefed.

5.2.2 Results

Data from four participants was removed from the analysis for failing to demonstrate a clear posing bias. A 2 x 2 Chi-square analysis revealed no influence of posing condition (family portrait, magazine cover portrait) on posing direction (left-cheek, right-cheek); χ^2 (1, N = 70) = .038, p = .845, φ = .023. As highlighted in Table 1, participants showed a tendency to reveal the right cheek regardless of posing condition.

A Chi-square analysis to examine overall posing direction demonstrated that the observed tendency was not significant; χ^2 (1, N = 71) = 3.169, p = .075, φ = .211. An additional 2 x 2 Chi-square analysis revealed no influence of participant sex (male,

female) on posing direction (left-cheek, right-cheek); χ^2 (1, N = 71) = .003, p = .960, φ = .006.

Table 5.1. *Frequency of left-cheek and right-cheek poses by gender and posing condition*

Sex	Condition	Left Cheek	Right Cheek	% Left
Male	Family Portrait	2	5	29
	Magazine Cover Portrait	4	4	50
Female	Family Portrait	12	18	40
	Magazine Cover Portrait	10	16	38
Total	Family Portrait	14	23	38
	Magazine Cover Portrait	14	20	41

5.2.3 Discussion

Although not statistically significant, there was a trend for participants to pose with the right cheek forward in both posing conditions. Where the rightward trend could suggest some intuitive understanding of the rightward attractiveness asymmetry, the failure to replicate the leftward posing bias for the family portrait scenario suggests that either 1) the data more likely reflects an error or the presence of an additional influencing variable, or 2) the family portrait posing condition does not result in a consistent leftward posing bias across replications. Concerning the former explanation, some potential issues with the data collection location may have influenced participant behaviour. For example,

participants were tested in small room off a busy classroom hallway. It is possible that the sound of people outside the door may have made the participants feel self-conscious and subsequently affected posing their behaviour; the rightward posing trend may reflect participants choosing to position themselves in a way to minimize the expression of their discomfort by displaying the less emotionally-expressive right cheek. Four participants noted that they felt awkward posing for the camera for the study. Concerning the latter explanation, Nicholls et al. (1999) report the only instance where the distinction in posing direction was manipulated with different posing scenarios. It remains a possibility that others have attempted and failed to replicate this finding, but that those failures to replicate were not published (Kennedy, 2004; Rosenthal, 1979).

5.3 General Discussion

The leftward posing bias in portraiture is well established in the literature, as is the influence of emotional expressivity on posing direction. Similar to emotional expressivity, facial asymmetry appears to show a rightward bias, but does that bias also influence posing behaviour?

In our examination of posing bias in modeling headshots, we predicted a rightward posing bias revealing the more attractive right cheek as the purpose of the modeling headshot is to highlight the attractiveness of the model. Our findings, however, confirmed the long-established left-cheek bias. When we examined posing behaviour directly, we failed to find a significant bias. Additionally, where posing biases are typically found to be greater for females, we failed to find a significant sex difference in either the modeling headshot images or in the posing behaviour for the family portrait or Vogue cover shot scenarios.

One possible explanation for the leftward posing bias observed for modeling headshots is that facial attractiveness does not influence posing bias. Although both emotional expression and attractiveness act as communication signals to foster social interaction (Chatterjee, Thomas, Smith, & Aguirre, 2009; Dunstan & Lindell, 2012; Schmidt, & Cohn, 2001), it is possible that we are intuitively aware of, and influenced by, the asymmetry in emotional expression but not by the asymmetry in facial attractiveness.

A second possibility is that we are intuitively aware of the attractiveness bias in facial physiognomy, but other factors play a greater role in determining the aesthetic preference in photo selection. Although the facial physiognomy of the right cheek might convey more attractive features, factors such as emotional expression (Nicholls et al., 1999), aesthetic appeal of the overall portrait (Christman & Pinger, 1997), scanning bias (Nachshon, Argaman, & Luria, 1999; Perez Gonzalez, 2012), and the left visual field and right hemisphere bias for facial processing (Levine, et al., 1988; Levy, et al., 1983) may all play a role in leading observers (e.g. photographers and the people who select images for publication) to choose a leftward pose as being more attractive or appealing overall. Portraits, although dominated by the subject, convey more information than simple attractiveness. Perhaps greater emotional expression rather than less is more aesthetically pleasing; perhaps the presence of features in the left side of the visual field results in a better flow or more efficient and fluent processing of the information contained within the portrait. Each of these influences may contribute, in varying degrees, to a general preference for leftward poses despite a rightward bias in facial attractiveness.

Related to this point, it is possible that a leftward posing bias was observed for the modeling headshots because a lack of prominent asymmetry in the models' features

necessitated the use of other factors to guide image selection. Attractiveness is often associated with greater facial symmetry (Fink, Neave, Manning, & Grammer, 2006; Mealy, Bridgestock, & Townsend, 1999), as models are generally highly attractive individuals, it may be possible that the degree of asymmetry between the left and right sides of their faces is not sufficient to judge one side as being more attractive. The leftward posing bias observed for this group may, then, be due to the influence of other factors on aesthetic judgment as a result of the high degree of symmetry.

A final possibility is that the right cheek is simply not the most attractive cheek. Although Zaidel et al. (1995) found that right-side composite faces were found to be more attractive than left-side composite faces, it is possible that composite faces are not representative of real faces as they provide an unbalanced representation of facial physiognomy, as information from only one hemiface is presented on both halves of the composite image. This overrepresentation of information from one side of the face produces an image that is easily distinguished from real face (Dunstan & Lindell, 2012). An attractiveness bias for the right cheek was observed for painted portraits of females (Zaidel & Fitzgerald, 1994), but attempts to replicate this result have been less successful. Blackburn and Shirillo (2012) measured participants' pleasantness ratings and pupil dilation in response to photographed portraits. Both measures revealed higher ratings of pleasantness in response to left-cheek images compared to right-cheek images, suggesting that the left side of the face is more aesthetically pleasing than the right. Further, Dunstan and Lindell (2012) found that the left side of males' faces were found to be more attractive both in the original and mirror-reversed orientations. Female faces, on the other hand, showed a mixed result, with the right side being rated as more attractive

when the face was presented in its original orientation and the left side being rated as more attractive when presented in its mirror-reversed orientation. This pattern of results suggests that any preference for one side of the female face is more likely due to a visual field bias than a true difference in facial physiognomy.

In general, posing bias research either examines images that have already gone through a selection process or the direct posing behaviour of participants asked to pose for a photograph. It may be that the model posing for the photograph intuitively knows that his or her right cheek is more attractive, but the final modeling headshot chosen to represent the model may highlight a left cheek due to a more attractive overall image presentation. In order to more fully understand the factors that drive the observed posing biases across the literature, the selection process needs to also be examined by asking participants to view a selection of left-cheek and right-cheek poses for a single model and select which image of the model is more attractive and which image is more aesthetically pleasing overall.

By eliminating the biases introduced by image selection for online publication and examining posing behaviour directly, we attempted to discern whether an intuitive awareness of the rightward attractiveness asymmetry would bias participants to pose with the more attractive right cheek forward. Although the non-significant trend suggested a rightward bias might be present, the failure to replicate the consistent leftward posing bias for the family portrait condition calls the overall results into question. Future research is still needed to discern 1) whether attractiveness can influence posing direction in the same manner as emotional expressivity, and 2) which factors influence the posing

behaviour of the subject of the portrait directly and which factors assert their influence through the artist's direction or the image selection process.

6. Experiment 5: Lateral Bias in Theatre-seat Choice[3]

From invertebrates to birds and mammals, examples of population-level lateral asymmetries can be observed across a wide range of behaviours (Tommasi, 2009). For example, in many species, there is a clear preference to use the right eye when feeding or approaching prey (Andrew, Mench, & Rainey, 1982; Güntürkün, 1997; Robins & Rogers, 2004; Rogers, 1997), or a faster response to the appearance of a predator when viewed with the left eye (Lippolis, Bisazza, Rogers, & Vallortigara, 2002; for a review see Bisazza, Rogers, & Vallortigara, 1998 and Vallortigara & Rogers, 2005). Similar asymmetries are also observed for a wide range of behaviours in humans despite an overall bilateral symmetry (Palmer, 2004); perhaps the most obvious of these behavioural asymmetries is handedness. Approximately 90% of the population relies predominantly on the right hand for fine motor tasks such as writing (Gilbert & Wysocki, 1992). Other, less obvious, asymmetries in human behaviour include the tendency to turn right upon entering a room (Scharine & McBeath, 2002), the tendency of people to turn to the right when kissing (Barrett, Greenwood, & McCullagh, 2006), and the tendency of people to choose seats to the right of the screen when asked to select their preferred seating location in a movie theatre.

Original studies on seating bias were based on observation of a bias in classrooms. Farnsworth (1933) found that more successful students tended to choose seats near the front of the classroom, a little to the right of center. Although Farnsworth argued that external factors such as window placement or the location of the teacher

[3] Published: Harms, V.L., Reese, M., & Elias, L.J. (2014). Lateral bias in theatre-seat choice. *Laterality, 19,* 1 -11.

influenced this lateralized bias, it is now understood that differences between the two hemispheres of the brain in processing specific kinds of information can lead to corresponding asymmetries in behaviour.

Asking participants to select movie theatre seats from a seating chart, Karev (2000) found that right-handed participants were more likely to choose a seat on the right side of the theatre than on the left side. This bias was reduced but not reversed in mixed- and left-handed participants. Karev proposed that the right-side seating bias reflects an advantage for right-hemisphere processing of visuospatial and emotional information (Bryden, 1982; Corballis, Funnell, & Gazzaniga, 2000). Theatre patrons would anticipate these processing demands and chose seats to maximize information processing efficiency. Right-side seats are preferentially chosen because they position the screen within the left visual field, which projects information to the right hemisphere for processing.

Using a similar procedure, Weyers, Milnik, Muller, and Pauli (2006) also confirmed the right-side bias observed by Karev (2000); however, when the theatre was presented in a non-canonical perspective, the right-side seating bias was reduced or eliminated. They also found an overall right-side-of-paper bias in seat selection. When the screen was not positioned at the top of the paper, as is standard on seating charts, participants were more likely to choose a seat on the right side of the page as opposed to the right side of the theatre. Weyers et al. argued against Karev's expectancy hypothesis, and proposed that the observed right-side seating bias is likely due to general right-side preferences such as turning preferences or visual-attention orientation.

Revisiting Karev's (2000) expectancy hypothesis, Okubo (2009) manipulated motivational and emotional factors in order to assess their influence on seating bias. When right-handed participants were positively motivated to see the movie, a right-side bias was observed in seating choice. This right-side bias disappeared when participants were negatively motivated to see the movie. Presentation of additional information suggesting that the movie was sad and depressing did not influence the direction of the seating bias. Okubo argued that this pattern of results is consistent with an expectancy effect.

One commonality between these theatre-seating studies is the use of paper seating charts for determining seat-choice. The assumption is that seat-choice from a chart or map accurately reflects real-world seat-choice behaviour, yet there are certain biases and influences that might affect seat choice differently between seating charts and actual seat location. For one, handedness is often suggested as an influence of seating choice in the seating chart studies. But, is it influencing seating choice due to its reflection of hemispheric asymmetries, or is it simply a bias to choose the same side of the page as your writing hand? These seating chart studies have provided informative insight into seat-choice behaviour and what might influence our choices, but what is not yet established is whether or not the right-side seating bias observed with seating charts is an accurate reflection of real-world seating choice. This present study examines whether a right-side bias is observed when people are free to choose their seating position in an actual movie theatre. If the seating-chart studies accurately reflect seat-choice behaviour, then a right-side seating bias should be observed in the naturalistic observation of seat selection.

Although the right hemisphere is generally thought to be the dominant hemisphere for emotional processing (Borod, Koff, & Caron, 1983; Borod, et al., 1998; Suberi & McKeever, 1977), there is some evidence to suggest that the left and right hemispheres play different roles, with the former responsible for positive or approach emotional processing and the latter responsible for negative or withdrawal emotional processing (Ahern & Schwartz, 1979). For example, the valence model posits that the left and right hemispheres govern the processing of positive and negative emotional information, respectively (Ehrlichman, 1987; Silberman & Weingartner, 1986). Lesion studies provide some evidence of a left-hemisphere role in emotional expression. Patients with right-hemisphere damage were found to experience more positive mood changes compared to patients with left-hemisphere lesions (Sackheim, et al., 1982). Conversely, patients with left-hemisphere damage show greater rates of depression following injury compared to patients with right-hemisphere damage (Robinson & Price, 1982). This pattern has similarly been demonstrated using sodium amytal testing, with left carotid artery injections resulting in negative emotional experience and expression, and right carotid artery injections resulting in positive emotional experience and expression (Perria, Rosadini, & Rossi, 1961; Rossi & Rosadini, 1967; Terzian, 1964).

Similar to the valence model, the approach-withdrawal model also posits a differentiation between the hemispheres, with the left hemisphere dominant for processing emotional information that will elicit approach behaviour and the right hemisphere dominant for processing information that will elicit withdrawal behaviour (Davidson 1995; Davison, Ekman, Saron, Senulis, & Friesen, 1990; for a detailed review of emotional lateralization see Demaree, Everhart, Youngstrom, & Harrison, 2005).

Evidence in support of this model, Davison et al., (1990) used EEG to measure arousal in response to video images designed to elicit either approach behaviour or withdrawal behaviour. They found greater right-hemisphere arousal in frontal and temporal areas in response to the withdrawal stimulus compared to the approach stimulus. This same pattern has been observed in non-human animal behaviour as well. Examining approach and withdrawal behaviour in dogs, Quaranta, Siniscalchi, and Vallortigara (2007) found more rightward tail-wagging movements in response to stimuli that should elicit approach behaviour and more leftward tail-wagging movements in response to stimuli that should elicit withdrawal behaviour. Similarly, Siniscalchi, Sasso, Pepe, Vallortigara, and Quaranta (2010) measured head-turning behaviour in dogs and found a consistent leftward turning bias in response to withdrawal stimuli.

To account for the differing biases that are predicted by the right-hemisphere hypothesis and the theories that propose differentiation of processing between the left and right hemispheres, we also examined the potential influence of expected emotional content by examining the influence of movie-genre on seating position. Although all movie genres touch on the full spectrum of emotions, the comedy genre aims to elicit more positive emotions in order to provoke a laughter response from the viewer whereas the dramatic genre aims to elicit more negative emotions to provoke a sense of pity or empathy in the viewer. Documentaries aim for emotional middle-ground, seeking to reflect real-life experience through a balance of positive and negative emotional content (Carroll, 2003; Gross & Levenson, 1995). If the left and right hemispheres do, indeed, play separate roles in processing emotional information, then the expected emotional content of the film (as indicated by the film genre) should influence the direction of the

observed seating bias, with dramatic films (associated with more negative emotional content) showing a right-side bias and comedies (associated with more positive emotional content) showing a left-side bias. Documentaries, with their balanced emotional content, would be expected to show a null bias. If the right hemisphere is dominant for processing emotional information, regardless of emotional valence, then the genre of the movie should not influence the observed seating-bias, and an overall right-side bias should be observed.

6.1 Method

6.1.1 Participants and Procedure

The seating position of movie-theatre patrons was photographed from the projection booth of a movie theatre. The photographs were taken prior to the start of the previews for the film. In order to ensure that a limited number of available seats did not influence seat choice, only movies with an attendance rate of 50% or less were used. A total of 32 images were collected. As this was a naturalistic observation study, participants in the study were unaware that their seat choice was being recorded.

The theatre where data collection was carried out screened predominantly independent films. The theatre featured a symmetrical layout. Two rear doors opened to two aisles located to the left and right of a center bank of seats (12 seats per row). A smaller bank of seats (5 per row) was located on the opposite side of each aisle. The seats were evenly divided between the left and right halves of the row, with no center seat. Two entrance doors were located at the rear-left and rear-right of the theatre, equidistant from the concession.

6.1.2 Data Coding

Two volunteers blind to the hypotheses of the study carried out image coding. The overall seating bias was calculated by counting the number of people seated on the right and left sides of the theatre separately. A bias score was then calculated by subtracting the number of left-seated patrons from the number of right-seated patrons. Thus, a positive score would indicate a right-side bias whereas a negative score would indicate a left-side bias. Each photograph was then assigned an overall bias rating (-1 for left-side bias, 1 for a right-side bias, and 0 for no bias). As it has been suggested that including the patrons seated in the central seats may artificially inflate the differences between the patrons who choose right-side seats and the patrons who choose left-side seats (Karev, 2000), a second set of bias scores excluding the four center seats of each row (center-removed seating bias) were calculated to test for this effect.

The genre of the movie for each image was coded by accessing the film information on the Internet Movie Database (imdb.com) and was classified according to the first entry in the genre category for the movie listing. All movies were classified as comedy, drama, or documentary.

6.2 Results

6.2.1 Inter-rater Reliability

Analyses of the inter-rater reliability for the coding of overall seating bias (kappa = 1.000, $p < .001$, 95% CI = 1.000, 1.000) and center-removed seating bias (kappa = .945, $p < .001$, 95% CI = .839, 1.051) indicate that the ratings were reliable.

6.2.2 Seating Bias

For the overall seating bias, a chi-square analysis revealed a significant seating bias with right-biased images [n = 23; $\chi^2(2) = 23.688$, $p < .001$, $\Phi = .86$] occurring more frequently than left-biased images (n = 8). Only one image indicated no bias in seat choice. A second analysis conducted with the no-bias image removed confirmed that the right-side bias occurred more often than the left-side bias [$\chi^2(1) = 7.258$, $p = .007$, $\Phi = .48$]. Figure 6.1 shows the seating-density pattern across all images, and Figure 6.2 shows the distribution of difference scores for all images. For the center-removed seating bias, the three seating positions were not found to be equally distributed [$\chi^2(2) = 8.313$, $p = .016$, $\Phi = .51$] with right-side biased images (n = 18) outnumbering left-side biased images (n = 5) and images with no bias (n = 9). To assess the difference between left- and right-biased images, the no bias images were removed. The chi-square analysis again revealed a significant right-side bias [$\chi^2(1) = 7.348$, $p = .007$, $\Phi = .57$]. This result confirms that the right-side bias observed is not due to artificial inflation of the bias scores. Together, these results indicate a significant right-side bias in seat choice for theatre patrons.

6.2.3 Influence of Movie Genre

We examined the potential influence of expected emotional content on seat-choice behaviour by testing the independence of movie genre (comedy, drama, or documentary) and seating-bias (left, right). A 3 x 2 Fisher's exact test indicated that seating bias was not influenced by movie genre (Fisher's exact test = 1.866, $p = .477$; see Table 2). A similar pattern of results was observed for the center-removed data; the

observed bias was not found to be significantly influenced by movie genre (Fisher's exact test = 1.619, p = .563; see Table 3). These results indicate that any differences in expectation of emotional content of the film based on genre did not significantly influence seating position.

Table 6.1. *Numbers of left-bias, right-bias, and no-bias images for all data*

Film Genre	Left Bias	Right Bias	No Bias
Comedy	0	5	0
Documentary	4	10	0
Drama	4	8	1

Table 6.2. *Numbers of left-bias, right-bias, and no-bias images for center-removed data*

Film Genre	Left Bias	Right Bias	No Bias
Comedy	0	5	0
Documentary	3	7	4
Drama	2	6	5

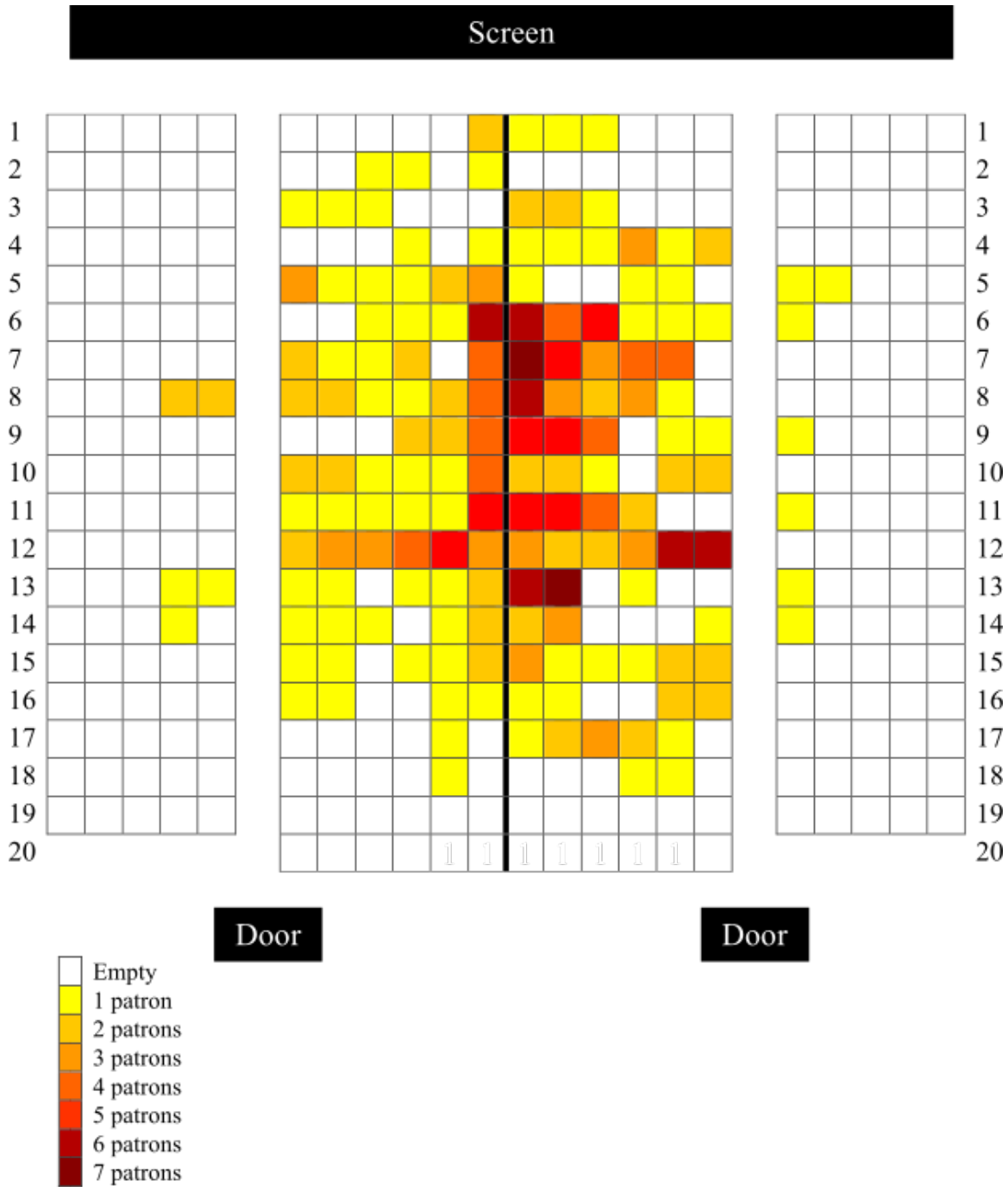

Figure 6.1. Seating chart showing the density of patrons' seating-choices across all images.

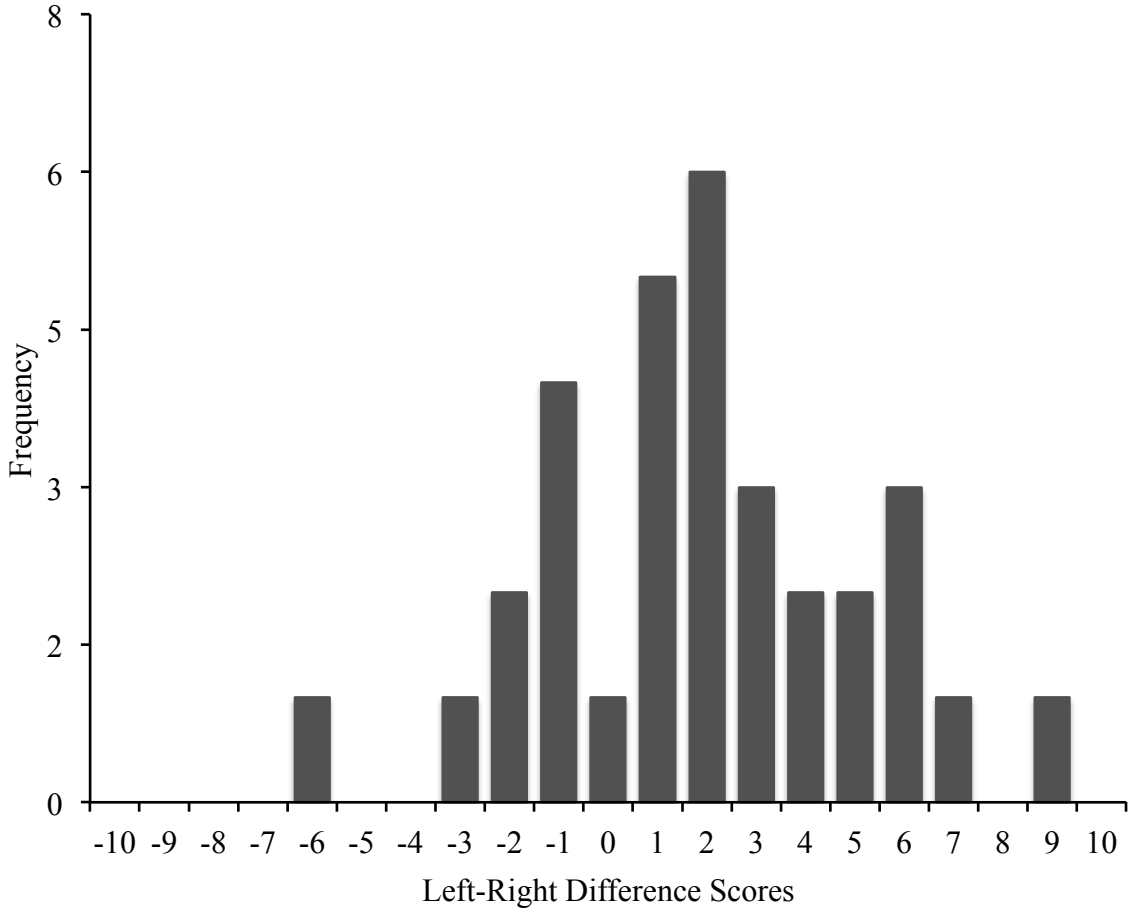

Figure 6.2. A frequency distribution of the difference scores calculated by subtracting the number of right-seated patrons from the number of left-seated patrons (left-right) is shown. Negative values indicate a left-side seating bias. The number of patrons in the photographs ranged from 1 to 30 with a mean of 10.2 (S.D. = 7.0).

6.3 Discussion

The results from previous research using seating charts suggested the presence of a right-side seating bias. These findings were confirmed in this real-world examination of seat-choice behaviour. A significant bias to choose seats on the right side of the theatre was observed, with a greater number of right-side sitters observed more often than a greater number of left-side sitters. The consistent observation of a significant right-side bias when all data was included and when the center seats were excluded provides strong evidence that our results are reflective of a true right-side seating bias and not due to an artificial inflation of the difference between right- and left-seated patrons.

The observed seating bias in the present study was not found to interact with the genre of the film. This particular theatre was chosen for its symmetry in the entrance position and orientation as well as the layout of the theatre itself so as to control for any external factors that might influence seating position within the theatre. As a theatre that specializes in independent films, it is possible that the expectations of emotional content would be different, as independent films are more likely to cross genre boundaries than are mainstream Hollywood productions (King, 2005; Tzioumakis, 2006). Further examination of the influence of genre on the theatre-seating bias with a focus on the more predictable and genre-focused Hollywood productions would provide a fuller picture of the role that movie-genre plays in seat-choice behaviour.

Karev's (2000) expectancy hypothesis predicts a right-side bias when choosing a seat in a movie theatre in order to maximize the processing efficiency of the expected visuospatial and emotional content of the film. If Karev's hypothesis is accurate, and seating bias is mediated in part by emotional lateralization, then potential differences in

the lateralization for processing negative and positive emotional stimuli could result in different seating-bias patterns as a result of the expected emotional content of the movie being viewed. The right-hemisphere hypothesis proposes that the right hemisphere is dominant for the processing of all emotional information (Borod, Koff, & Caron, 1983); however, there is also some evidence to suggest a left-right division of emotional processing, with the left hemisphere governing positive or approach emotional processing and the right hemisphere governing negative or withdrawal emotional processing (Ahern & Schwartz, 1979; Davidson 1995; Davidson et al., 1990; Ehrlichman, 1987; Silberman & Weingartner, 1986). The results reported here indicate that movie genre did not influence seating bias. This result may indicate a right-side dominance for emotional processing in general as the bias is not sensitive to differences in the type of emotional content expected, or it may indicate the preferential influence of visuospatial information over emotional content. Karev (2000) suggested that it was the right-hemisphere dominance for both visuospatial and emotional processing that biased seating position but he did not predict to what extent each of these processing functions contributed to the bias. It is possible that the right-hemisphere contributions to emotional processing and visuospatial processing each influence the seating bias to a different degree. Further examination is needed to tease apart these possibilities.

As an alternative explanation to Karev's (2000) expectancy hypothesis, Weyers et al. (2006) suggested that the right-side seating bias may be mediated by an overall preference to turn right upon entering a room (Scharine & McBeath, 2002); with a single entrance centered at the back of the theatre, a right turn upon entering the theater places the participant on the right side of the theatre. As the theatre in the present study featured

two lateralized entrances at the rear-left and rear-right of the theater (both located equidistant from the concession in the theatre lobby), it is unlikely that turning habits can fully explain the right-side bias; entering the theater through the left-side door and turning right would result in a seat-choice on the middle-left side of the theatre unless the patrons walk across the aisle to the right side of the theatre. Similarly, upon entering the theatre through the right-side door, a right-turn bias would position patrons for choosing seats on the far-right aisle compared to the right side of the middle aisle. A comparison of the two locations indicates a greater preference for the middle-right compared to the far-right at a ratio of approximately 28:1. This pattern suggests that the right-side seating bias is mediated, at least in part, by influences other than turning-bias.

6.4 Conclusion

This present study of real-world seat-choice behaviour confirms the right-side seating bias observed in prior research and provides evidence that seating-chart seat selection accurately reflects seat-choice behaviour in a real-world context. These results demonstrate a significant preference for choosing seats on right side of the theatre, and they suggest that this seating bias is not dependent on the expected emotional content (as indicated by genre) of the film being viewed.

7. Experiment 6: Take Your Seats: Leftward Asymmetry in Classroom Seating Choice

Despite an overall bilateral symmetry in body morphology, humans display a wide range of motor and perceptual asymmetries (Palmer, 2004; for a review, see Brancucci, Lucci, Mazzatenta, & Tommasi, 2009). Handedness is perhaps the most obvious of these behavioural asymmetries, with approximately 90% of the population displaying a right-hand dominance for writing and the execution of other fine motor tasks (Dragovic, 2004; Gilbert & Wysocki, 1992). Less obvious examples of behavioural asymmetries can also be observed, including biases to turn to the right when entering a room (Scharine & McBeath, 2002), kissing (Barrett, Greenwood, & McCullagh, 2006), presenting the left cheek when posing for a portrait (Nicholls, Clode, Wood, & Wood, 1999), or leaning in with the right ear to hear a conversation in a noisy environment (Marzoli & Tommasi, 2009). In addition to these asymmetries, people also exhibit seating asymmetries in movie theatres, airplanes, and classrooms (Harms, Reese & Elias, 2014; Nicholls, Thomas, & Loetscher 2013; Farnsworth, 1933).

Karev (2000) noted a personal observation that seats on the right side of theatres were chosen more frequently than seats on the left. To test this observation, Karev asked participants to select their preferred seating location in a movie theatre from a seating chart of available seats. With the middle seats marked as unavailable, participants were forced to select a seat to the right or left side of the theatre. Consistent with his initial observation, Karev found an overall bias for people to choose seats on the right more often than seats on the left. Although the bias was strongest for right-handed participants, the bias was attenuated, but not reversed, in left- and mixed-handed participants. To

explain this asymmetrical seating bias, Karev argued that people, expecting specific processing demands, choose a seating position that will maximize the processing efficiency of the anticipated information content. Seats to the right are preferred in a movie theatre because they position the screen to the left side of the visual field, allowing for efficient processing of the film's visuospatial and emotional content in the right hemisphere (Bryden, 1982; Corballis, Funnell, & Gazzaniga, 2000).

To test Karev's (2000) expectancy hypothesis, Okubo (2009) manipulated both the level of motivation to see the film and the anticipated emotional processing demand of the participants to evaluate their influence on seating behaviour using seating charts. A rightward seating bias was observed when right-handed participants were positively motivated to view the film and was absent when right-handed participants were not motivated to view the film. Additionally, when participants were specifically informed that the film contained negative emotional content, the rightward bias was again observed for right-handed participants who were positively motivated to view the film (Okubo, 2009). Okubo argued that these results were consistent with Karev's (2000) hypothesis that an expectation for emotional processing would bias participants to choose seats to the right.

Using a method similar to Karev (2000), Weyers, Milnik, Mueller, and Pauli (2006) examined seating behaviour using both the standard seating chart (with the screen positioned at the top of the page) and non-standard seating charts (with the screen positioned either to the far right, the far left, or at the bottom of the page). Consistent with Karev's (2000) findings, a rightward seating preference was observed for the standard seating chart. This bias was reduced or eliminated when seats were selected from non-

standard seating charts; additionally, Weyers *et al*. (2006) observed a tendency for participants to choose seats to the right side of the paper when selecting a seat in a cinema. Weyers *et al*. argued that the observed bias patterns reflect general right-side motor biases and preferences such as a preference for turning to the right upon entering a room.

A common theme across these studies is their reliance on seating-charts. They rely on the assumption that the seat selected when imagining where one would sit in a theatre is equivalent to the seat that would be selected when one actually goes to the movies. Addressing this issue, two real-world studies have examined the seating behaviour of actual theatre patrons. Nicholls, *et al.* (2013) assessed the seating preferences of theatre patrons by counting the number of purchased seats for theatre performances booked through Ticketmaster online. Consistent with the seating chart studies, a rightward seating bias was observed for performances at 50% capacity or below. Similarly, Harms, *et al.* (2014) photographed the seating position of movie theatre patrons at actual film screenings. Again, consistent with the seating chart studies, a significant bias for patrons to select seats to the right side of the theatre was observed.

Although much of the seating bias research has focused on a theatre setting, additional studies have examined the influence of seating position in the classroom on academic performance. For example, Farnsworth (1933) noted that academic success was correlated with classroom seating position, with the most successful students seated near the front of the classroom, slightly to the right of center. Similarly, in an examination of spelling performance in children, Morton and Kerschner (1987) found that students seated on the right side of the classroom made less spelling errors compared to students

seated on the left side of the classroom. An analysis of the types of errors made led the authors to suggest that right-side sitters and left-side sitters employed different processing strategies for completing the spelling test. To further examine the relationship between seating bias and processing strategy, Morton, Wearne, Kerschner, and McLean (1993) evaluated how the degree of reliance on specific learning styles varied with seating position in adult participants. Overall, right-sitters were found to rely on responses that showed more artistic or holistic processing and less analytical processing compared to left-sitters. Left- and right-sitters were found to rely on learning styles that emphasized left- and right-hemisphere dominant processes, respectively. For example, left-sitters were found to perform more accurately on dichotic listening tasks using CVC and digit stimuli than right-sitters, reflecting the left hemisphere advantage for verbal processing (Bryden, 1982; Kimura, 1967).

Employing a similar method to Harms *et al*. (2014), this present study examines the real-world classroom seating preferences of university students. The examination of seating preferences within a classroom setting offers us an opportunity to directly test the competing explanations for seating biases proposed by Karev (2000) and Weyers *et al*. (2006). Whereas movies are expected to provide predominantly visuospatial and emotional content, university classes are predominantly lecture-based and, thus, are expected to provide predominantly visual and auditory verbal content requiring analytical processing (Ballantyne, Bain, & Packer, 1999). Mathematical information (Pinel & Dehaene, 2010), analytical processing (Bever, 1975), and verbal processing (Kimura, 1961) have all been shown to demonstrate left-hemispheric processing advantages. This expectation of left-hemisphere dominant processing demand for university classes gives

rise to opposing seating behaviour predictions from Karev's expectancy hypothesis and Weyers et al.'s (2006) hypothesis that motor asymmetries, such as turning biases, govern seating biases, affording us the opportunity to directly compare their predictions on real-world behaviour.

If Karev's (2000) expectancy hypothesis is accurate, then it follows that an expectation for predominantly verbal and analytical content that is preferentially processed in the left hemisphere should result in a leftward seating bias, as this seating position places the instructor and the projector screen in the right visual field and positions the right ear towards the center of the classroom and the source of the auditory information. This position allows the incoming visual and auditory information to be routed efficiently to the left hemisphere for processing. If the expectation of specific processing demands is what drives seat-choice behavior, then we should see an overall preference for students to choose seats to the left side of the classroom. Alternatively, if Weyers *et al*. (2006) are correct, and seating biases are more simply a reflection of basic motor biases, then it follows that the difference in expected processing demand between movies and lectures should not influence the seating bias at all. In that case, students in university classrooms should then show the same right side seating bias observed among movie theatre patrons.

7.1 Method

7.1.1 Participants and Procedure

To assess the seating bias observed in classroom seating, the seating position of the students was photographed in lecture halls and classrooms across the University of Saskatchewan campus. Images were collected from the center back of the classroom or

lecture theatre. The focal length of the lens was adjusted for each image to ensure that all seats in the room were visible in the photograph. The images were taken approximately five minutes prior to the start of the class. To ensure that limited availability of seats did not unduly influence seat choice, only classrooms with occupancy rate of 50% or less at the time the photograph was taken were used. A total of 41 images were collected from 41 different classes in 29 different classrooms across campus. As this study used the naturalistic observation method, the students in the study were unaware that their seating position was being recorded.

7.1.2 Data Coding

A volunteer blind to the hypotheses of the study carried out image coding. The overall seating bias was calculated by counting the number of people seated on the right and left sides of the classroom separately. A laterality index was then calculated by subtracting the number of left-seated students from the number of right-seated students. Thus, a positive score would indicate a right-side seating bias whereas a negative score would indicate a left-side seating bias. Each photograph was then assigned an overall seating bias rating (-1 for left-side bias, 1 for a right-side bias, and 0 for no bias).

In addition to the bias rating, classroom entrance position and location of the center seat were also recorded. Using the floor plan for each classroom or lecture hall where an image was collected, the lateral position (left, right, or bilateral) and axial position (front or back) of the entrance(s) was recorded. The location of the central seat was also recorded and used as the reference point for dividing seating position between the left and right sides of the classroom. Additionally, the subject of each class

photographed was recorded and coded as either an Arts or a Science class, according to the class description in the course calendar.

7.2 Results

7.2.1 Seating Bias

Examining the overall classroom seating bias, a Chi-Square analysis on the frequency of images per seating position category revealed a significant seating bias with left-biased images [n = 25; $\chi^2(2) = 16.439$, $p < .001$] occurring more frequently than right-biased images (n = 12) or no-bias images (n = 4). To further assess whether there was a significant difference in the frequency of leftward biased images compared to rightward biased images a second Chi-Square analysis was carried out with the no-bias images removed [$\chi^2(1) = 4.568$, $p = .033$]. These results indicate a bias for students to select seats to the left side of the classroom. The seating-density pattern observed across all images is presented in Figure 7.1. Additionally, a one-sample *t*-test was conducted to evaluate whether the overall laterality index across all images revealed a leftward or rightward bias. A significant leftward bias was observed [$t(40) = -2.999$, $p = .005$, 95% CI = -3.23, -.63, $M = -1.93$, $SD = 4.11$]. Figure 7.2 shows the frequency distribution pattern of difference scores across all images.

7.2.2 Influence of Entrance Location

As the images for the study were collected from a large number of classrooms, it is possible that variations in the location of classroom entrances may have influenced seat choice. Through post hoc analysis, we examined the potential influence of lateral entrance position on seat-choice behaviour by testing the independence of entrance location (left, right, or bilateral) and seating-bias (left, right). The four images showing

no bias in seating were removed for this analysis. A 3 x 2 Chi-Square test demonstrated no influence of lateral entrance position on classroom seating bias [$\chi^2(2) = .554$, $p = .758$, $V = .122$; see Table 4]. As there was only one left side entrance image collected, a 2 x 2 Chi-Square test with the left-side entrance location removed was used to assess whether asymmetrical (right-side) or bilateral entrance position influences seating position. Again, no influence of lateral entrance position on classroom seating bias was observed [$\chi^2(1) = .060$, $p = .806$, $V = .041$]. These results indicate that any differences in the lateral location of the entrance to the room did not significantly influence students' choice of seating position.

Table 7.1. *Numbers of left-bias and right-bias images for all lateral entrance positions*

Entrance Position	Left Bias	Right Bias
Left	1	0
Right	15	8
Bilateral	9	4

Additionally, the location of the entrance with respect to the front or back of the room has also been argued to influence seating position. We examined the potential influence of axial entrance position on seat-choice behaviour by testing the independence of axial position (front, back, or both) and seating bias (left, right). The four images showing no bias in seating were removed for this analysis. A 3 x 2 Chi-Square test demonstrated no

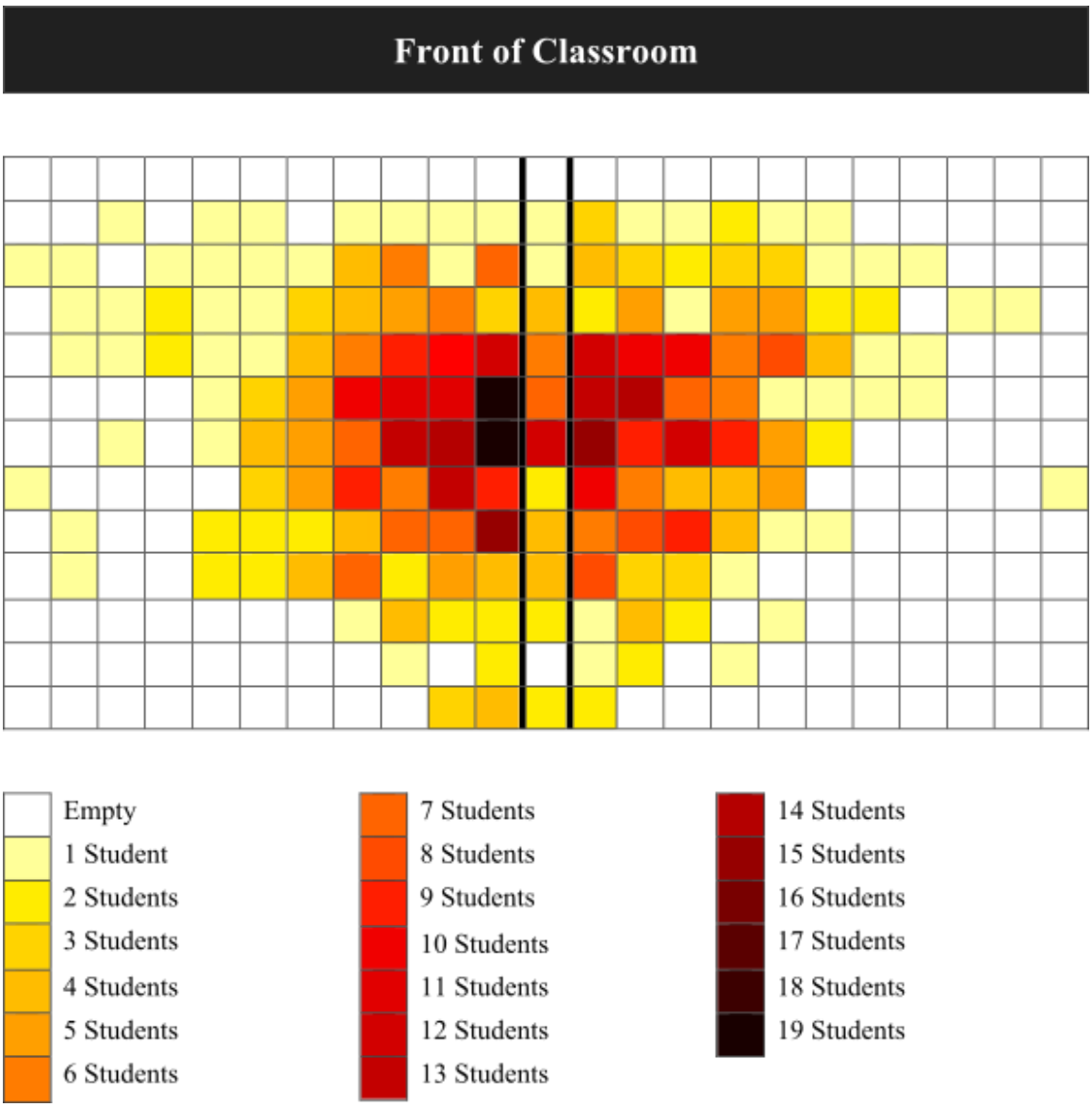

Figure 7.1. Normalized seating chart showing the density of students' seating-choices across all images. To correct for the differences in seating capacity across rooms, the seating position for each classroom was transposed such that the center seat of the classroom corresponded with the center seat of the seating chart grid.

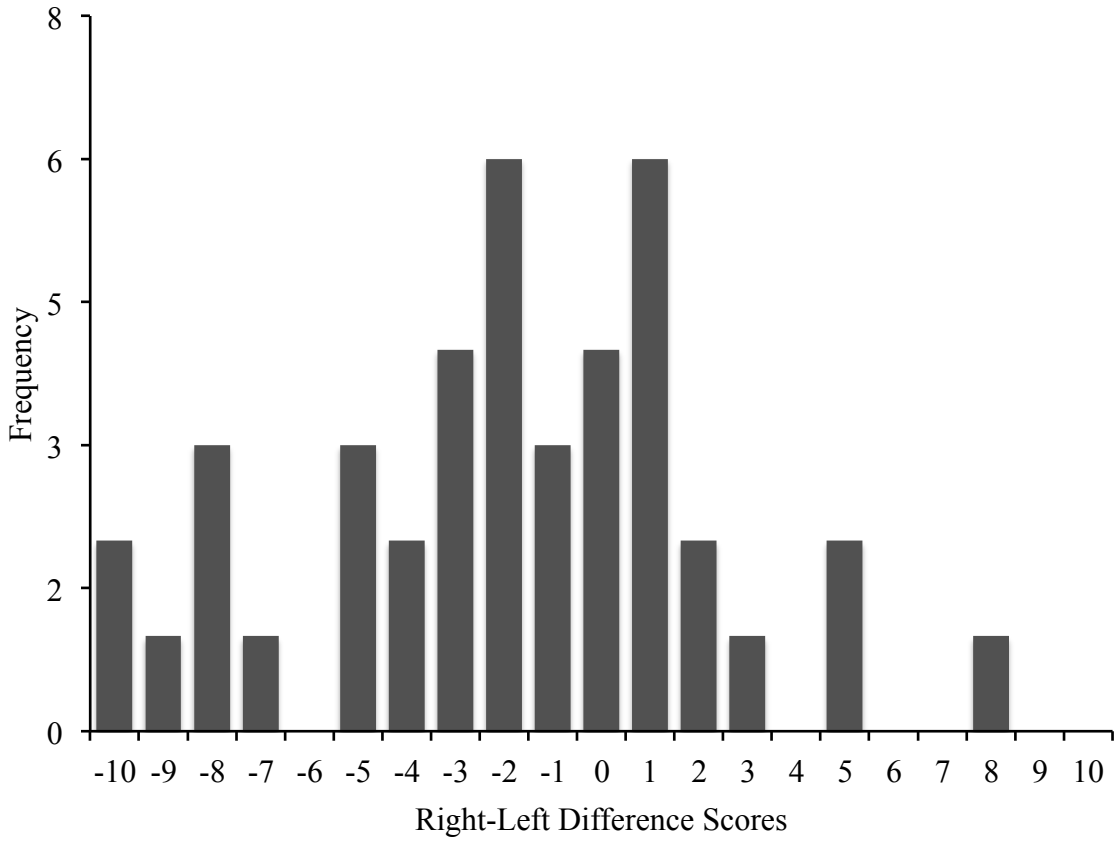

Figure 7.2. The frequency distribution of the difference scores calculated by subtracting the number of left-seated patrons from the number of right-seated patrons (right-left) is shown. Negative values indicate a left-side seating bias. The number of students in the photographs ranged from 1 to 55 with a mean of 17.07 (*SD* = 12.58).

influence of axial entrance position on classroom seating bias [$\chi^2(2) = .059$, $p = .971$, $V = .040$; see Table 5]. Similar to the results examining lateral entrance position, these results indicate that the presence of a front or rear entrance to the room did not significantly influence students' choice of seating position.

7.2.3 Influence of Class Type

Lastly, as processing demands may vary by subject matter, we examined the potential influence of course subject on seat-choice behaviour by testing the independence of class type (Arts, Science) and seating bias (left, right). The four images showing

Table 7.2. *Numbers of left-bias and right-bias images for all axial entrance positions*

Entrance Position	Left Bias	Right Bias
Front	10	5
Back	10	5
Both	5	2

no bias in seating were removed for this analysis. A 2 x 2 Chi-Square test demonstrated no influence of class type on classroom seating bias [$\chi^2(1) = .330$, $p = .565$, $V = .094$; see Table 6].

Table 7.3. *Numbers of left-bias and right-bias images for all class types*

Class Type	Left Bias	Right Bias
Arts	10	6
Science	15	6

7.2.4 Comparison of Theatre and Lecture Seating Data

To assess the overall influence of processing demand, we tested the independence of task type (theatre, lecture) and seating bias (left, right), combining the classroom seating data from the current study with the theatre seating data collected by Harms et al. (2014). Images showing no bias were removed for this analysis. A 2 x 2 Chi-Square test demonstrated a significant association between task type and seating bias where theatre seating images showed a greater rightward bias and classroom seating images showed a greater leftward bias [$\chi^2(1) = 11.777$, $p = .001$, $V = .416$; see Table 7].

Table 7.4. *Numbers of left-bias and right-bias images for theatre and lecture task types*

Task Type	Left Bias	Right Bias
Theatre	8	23
Lecture	25	12

7.3 Discussion

The difference in expected processing demand between movie theatres and university classrooms afforded us a unique opportunity to test two opposing explanations for the rightward seating bias observed in theatre seating studies. Karev's (2000) expectancy hypothesis predicted that the expectation of left-hemisphere dominant processing demands in the classroom setting would result in an overall leftward preference in seating position among university students, opposite to the rightward bias

observed among movie theatre patrons. Alternatively, Weyers *et al*.'s (2006) suggestion that rightward motor asymmetries, such as the tendency to turn right upon entering a room (Sharine & McBeath, 2002), dictates seating position preference predicted an overall rightward preference in seating position among university students.

Our naturalistic observation of the classroom seating position of university students revealed a preference for seats on the left side of the classroom, confirming the prediction of a leftward bias derived from Karev's (2000) expectancy hypothesis. This finding is complementary to Harms *et al*.'s (2014) observed preference for seats on the right side of the movie theatre using the same procedure as well as the rightward bias observed for online ticket purchases observed by Nicholls *et al.* (2013). Additionally, a direct comparison of the seating bias for theatre patrons and classroom students provided further evidence that the differing processing demands of the movie theatre and the classroom resulted in opposite seating biases. Together, these studies provide a body of evidence suggesting that lateralized processing asymmetries play a substantial role in governing seating preferences based on anticipated processing demands, with anticipated processing of left-hemisphere dominant verbal and analytical content (Kimura, 1961; Bever, 1975), resulting in a left side seating preference, and right-hemisphere dominant visuospatial and emotional content (Bryden, 1982; Corballis *et al.*, 2000) resulting in a right side seating preference.

The leftward bias for classroom seating is also consistent with Morton *et al*.'s (1993) finding that preferred seating position reflects preferred learning or response style. For example, they found that left-sitters performed more accurately on CVC and digit dichotic listening tasks compared to right-sitters. They argued that this result reflected a

greater reliance on left-hemisphere processing and learning or response strategies in left-sitters. Although the authors continued to suggest that actual seating position likely did not influence performance, other researchers have found visual field and ear advantages for a variety of stimulus processing tasks (e.g. Bryden, 1982, Cherry & Hellige, 1999; Kimura, 1961), suggesting that preferential positioning can improve processing efficiency.

Interestingly, our results do not fit with Farnsworth (1933) and Morton and Kerschner's (1987) findings of academic performance advantages for students seated on the right side of the room. We did not examine the relationship between seating position and performance, rather we simply examined seating preference in isolation. It may be that left-side seating provides a sense of greater processing fluency without providing a further advantage on a student's ability to recall or integrate the processed information on assigned tasks; alternatively, right-side seating may provide an attentional advantage that results in greater academic performance, despite a reduced processing fluency for verbal information, that results in improved performance on learning assessments. Additional research is needed to tease apart these possibilities.

We also assessed the potential influence of course differences on student seating position. Although we did not find an influence of general class type (arts or science) on seating bias, it may be that the processing demands vary by specific subjects, and that the optimal seating location to improve processing fluency may vary as a function of the topic or subject being covered beyond the general classification of Arts or Science. For example, an Engineering design course and a Fine Arts course may both require a greater reliance on visuospatial (right hemisphere dominant) processing due to the heavy reliance

on pictoral information. Similarly, both Mathematics and Lingusitics courses rely heavily on symbolic representation processing (left hemisphere dominant). Additional controlled analyses of the relationship between preference, performance, and the differential processing demands per subject or class type are needed to further clarify whether expectation of processing fluency is truly guiding factor in seating location choice among students.

It is worth noting that, besides differences in processing demand expectations, the social contexts surrounding a trip to the movies and attending class are substantively different. Whereas a trip to the movies is typically a social activity with most people attending with friends or family, many students attend classes alone. These contrasting social contexts may be influencing seating behaviour. It has been shown that behaviour changes based on social context (Berkowitz, 1972), for example, people tend to eat more food when dining with friends compared to dining alone (Hetherington, Anderson, Norton, & Newson, 2006). The social context of the setting may influence how seating location is determined. For example, when selecting a seat with a group of friends, an individual may forgo a preferred seating location to conform to the group preference. This need to conform is negated when an individual is selecting a seating location alone. An examination of seating behaviour in theatre and classroom contexts controlling for social factors is needed to assess the relative contributions of both social and processing expectancy factors on seating location asymmetries.

Additionally, personality characteristics such as anxiety level have been proposed as influencing factors in determining an individual's seating position. An early study by Gur, Sackheim, and Gur (1976) examined the relationship between seating location and

psychopathology in university students. They found that males seated on the right side of the classroom reported higher rates of psychopathology compared to males seated on the left. Conversely, they found that females seated on the left side of the classroom reported higher rates of psychopathology compared to females seated on the right. Similarly, Luck (2006) examined the relationship between seating position choice and psychological distress in patients during a medical consultation. He found a leftward seating bias in patients reporting high levels of anxiety or depression and a rightward bias among patients reporting low levels of anxiety or depression. Given these findings, it is possible that the students who arrived to class and were seated prior to the photographs being taken may be more anxious, and thus more likely to sit to the left side of the classroom. In discussing the potential influence of personality characteristics, it is worth noting that the student population tends to be less variable overall than the population of individuals who attend movies. Whereas university students tend to be young adults from middle-class backgrounds, theatre patrons show a greater age range, from children through to seniors, and come from a wider range of socioeconomic backgrounds. The context difference between attending a movie and attending a class also have the potential to influence variables such as the degree of anxiety experience, with class attendance likely resulting in higher levels of anxiety compared to movie attendance. An additional examination of the relationship between personality traits and seating position is needed to assess the degree to which anxiety or other personality characteristics might influence seating position.

Although these data provide evidence against the argument that turning biases or rightward motor asymmetries are responsible for the rightward seating biases observed in

the theatre-seating studies, it could be argued that the variety of entrance layouts reflected in the data set may have influenced the seating choices of the students. Entrance position, whether lateral or axial, was not found to interact with seating position. The left side seating bias was observed regardless of the position of the room entrance(s). The majority of classrooms had entrances located either solely to the right side of the room (27/41 = 66%) or bilaterally (13/41 = 32%). Only one classroom had a left-side only entrance (2%). Of the 27 right-entrance images, 15 showed a leftward seating bias revealing a greater preference for leftward seats compared to rightward seats at a ratio of 2:1. This suggests that students were willing to cross to the opposite side of the classroom from the right side, where they entered, to take a seat on the left side of the room. This counters the argument that people choose to sit on the side of the room where they enter. Taken together, these observations suggest that entrance position is not a significant factor in determining the location of seat choice within the classroom.

7.4 Conclusion

This naturalistic observation of classroom seating behaviour revealed a leftward seating asymmetry, complementary to the rightward asymmetry observed in studies of theatre seating. Consistent with the predictions derived from Karev's (2000) expectancy hypothesis, the data presented here suggests that lateral biases in seating location are likely not driven by basic motor asymmetries such as turning biases, but rather reflect a behavioural influence of asymmetrical hemispheric lateralization for information processing demands.

8. General Discussion

The experiments presented here were designed to explore: 1) the mechanisms that explain how and why the typical patterns of cerebral lateralization arose and 2) the consequences of these patterns of cerebral lateralization for our everyday behaviour. Experiments 1 and 2 tested the assumption made by many evolutionary theories of cerebral lateralization that there is a causal relationship between the lateralized processes of the left and right hemispheres. Experiments 3 through 6 examined the influences of those lateralized cognitive functions on behaviour.

8.1 Mechanisms

The degree and direction of lateralization observed for left-hemisphere language processing and the right hemisphere emotional (Experiment 1) and melodic (Experiment 2) processing were compared within individuals to assess what pattern of complementary relationship was observed. Despite its inherent assumption in most evolutionary theories of laterality, the causal model of complementarity was not supported by the data. Rather, consistent with the statistical model of complementarity, Experiment 1 revealed the expected population-level asymmetries in task performance, but demonstrated statistical independence when compared within individuals. The pattern is in keeping with the growing body of evidence supporting a statistical pattern of complementarity. As the expected population-level asymmetry for melodic processing was not found for the right-hemisphere task in Experiment 2, an assessment of the complementary relationship between melodic and linguistic processing could not be made.

Taking the results of Experiment 1 together with the small but growing number of studies examining complementarity, the evidence in support of a statistical relationship

between left- and right-hemisphere functions appears to be strengthening. All but one study have failed to find a significant negative correlation between left- and right-lateralized functions within individuals (Andresen & Marsolek, 2005; Hellige, Bloch, & Taylor, 1988; Ley & Bryden, 1982; McNeely & Parlow, 2001; Nestor & Safer, 1990; Rosch et al., 2012; Saxby & Bryden, 1984; Whitehouse & Bishop, 2009). The mounting evidence for statistical complementarity calls into question the majority of evolutionary theories that have been put forward to explain hemispheric functional asymmetry and demands an evolutionary explanation for laterality that does not rely on a causal mechanism.

Additional examination of the specific relationships posited by these evolutionary theories would provide more definitive evidence either for or against their specific predictions. For example, if language is posited to have a gestural origin, with the development of right-hand gesturing resulting in an evolved motor skill advantage in the left hemisphere that forms the foundation for language, then those individuals who show a left-hand preference for gesturing during speech should show right-hemisphere dominance for language processing. If these exceptions to the modal model reveal the reversed pattern of lateralization for language and gesturing (right-hemisphere dominance for linguistic processing and left-hand dominance for gesturing during speech), that would provide evidence in support of the causal assumption underlying that evolutionary explanation; however, as handedness has been shown to be a weak predictor of language lateralization (Day & MacNeilage, 1996; Rasmussen & Milner, 1977; Searleman, 1980), I would predict that the association between gesture hand and language lateralization

would reflect the pattern of statistical complementarity emerging in the literature rather than the causal pattern predicted by the gesture-based theories of cerebral lateralization.

With their Interhemispheric Conduction Delay hypothesis, Ringo and colleagues (1994) proposed an evolutionary mechanism that does not reply on a causal relationship between lateralized functions; however, the theory fails to account for the direction and consistency of functional asymmetry at the population level. The theories that do attempt to account for these factors do so through the assumption of a causal factor. A new model is needed that accounts for the statistical independence of the observed hemispheric asymmetries and proposes a mechanism that explains the pattern of asymmetry at the population level.

As Ringo *et al.* (1994) note, the delay in conduction time between the hemispheres may produce a significant enough lag in the temporal coordination of action to impact performance. If the mechanisms that controlled and coordinated complex and rapid temporal sequences of action were localized within a single hemisphere, the slight performance advantage in the production and implementation of a motor plan in response to harmful external stimuli could provide and evolutionary advantage. Similarly, the ability to rapidly integrate information from the senses, map the spatial location of objects in the environment, and compute their relationship to one's own position in the environment is essential to being able to accurately and efficiently guide the direction of action responses. Having these functions lateralized to the same hemisphere could then provide a timing advantage that would prove advantageous should quick timing and accurate spatial localization of action be required.

At the surface, this may seem similar to Kosslyn's (1987) Computational Theory, where he posits opposite lateralization of language and visuospatial attention allow for the two resource-intensive networks to function most efficiently. However, where Kosslyn predicts a causal relationship between the two functional networks, I suggest that both temporal sequencing mechanisms and spatial orientating and sensory integration mechanisms could be lateralized within the same hemisphere. Independent lateralizing forces for each function drive the lateralization of temporal sequencing and spatial attention. Rather than pinning the direction of lateralization of all functions in the brain on the initial shift of one function or set of functions to one hemisphere, I argue that each function or related set of functions is lateralized by an independent mechanism, and that the direction of lateralization of any one function is not influenced by the direction of lateralization of any other function.

This suggested approach to explaining the evolution of cerebral lateralization is consistent with the overall pattern of statistical complementarity observed across most examinations of individual patterns of hemispheric lateralization (Andresen & Marsolek, 2005; Hellige, Bloch, & Taylor, 1988; Ley & Bryden, 1982; McNeely & Parlow, 2001; Nestor & Safer, 1990; Rosch et al., 2012; Saxby & Bryden, 1984; Whitehouse & Bishop, 2009). Additionally, this approach is also consistent with research suggesting that atypical laterality profiles, those deviating from the modal model, show no evidence of processing disadvantages or deficits compared to the modal model (Knect *et al.*, 2001; Bishop *et al*, 2014). However, until a complete map of the relationships between lateralized functions is created, any evolutionary theory, even those that account for atypical laterality profiles and statistical complementarity, needs to be considered with

caution. Our knowledge of how the various lateralized functions are related is still limited, and any theory explaining how laterality evolved needs to consider all related functions, not reply on one function or subset of functions to explain the global pattern of lateralization.

The statistical complementarity theory suggests that most functions are lateralized at random. The occasional finding of a causal pattern between two or more functions may reflect that, within the overall pattern of statistical complementarity, there are subsets of functions that are lateralized by a common process. A comprehensive map of the relational network of all lateralized functions within the brain is ultimately needed to create a global picture of the evolution of cerebral lateralization. Once we understand what functions share a common lateralizing influence, and how many separate lateralizing influences there appear to be, we can begin sculpting a comprehensive evolutionary theory that accounts for the biases of all functions rather than isolating and elevating a single function of set of functions as the overall cause of cerebral lateralization.

For example, future directions in establishing an evolutionary theory of lateralization that takes into account the greater pattern of relationship between left- and right-hemisphere functions could include using transcranial magnetic stimulation (TMS) to assess the relative role of each hemisphere in processing performance on a battery of lateralized processing tasks within individuals. By directly assessing each hemisphere's contribution to a wide range of processing tasks such as spatial, linguistic, emotional, and temporal processing within the same individuals, and evaluating the relationship between the degree and direction of lateralization between each of those processes at the level of

the individual, we can take a first step towards creating a more comprehensive map differentiating between related and independent processes.

8.2 Consequences

Experiment 3 examined the influence of attractiveness on posing direction. Despite evidence suggesting a rightward bias in facial attractiveness, the overall trend in portraiture is to show the left side of the face. This experiment was designed to test whether changing the purpose of the portrait to specifically highlight the more attractive features of the subject would change the direction of the posing bias. Consistent with the posing literature, an examination of posing direction in modeling headshots revealed a leftward posing bias. Experiment 4 attempted to control for the possible influence of viewer selection biases, but a failure to replicate prior leftward biases in the control condition indicated the influence of an external factor on posing direction.

The leftward bias observed for modeling headshot images in Experiment 3 suggests an intriguing possibility. If evidence suggests that the right side of the face is more attractive, and the purpose of the image is to highlight attractiveness, intuitively, we should expect the right side of the face to be presented. In light of Nicholls et al.'s (1999) finding that posing behaviour is influenced by emotional expressivity and its control via lateralized motor and emotional processing functions, the failure to find a rightward bias might indicate that asymmetries in cognitive functioning are more influential in governing behaviour than asymmetries in physiognomy, even when the physiognomy bias may be more advantageous in controlling behaviour. It appears that influences of asymmetrical cognitive processing, whether emotional processing, scanning biases, processing of faces, or aesthetic preferences win out over simple facial physiognomy in

influencing posing direction for portraits even when attractiveness is the goal of the image.

Zaidel et al. (1995) found the right side of the face to be more attractive when participants were asked to focus specifically on facial attractiveness, yet when asked to rate the overall aesthetic pleasantness of an image, participants tend to prefer left-cheek poses (Blackburn & Schirillo, 2012). If magazine editors or modeling photographers select images based on the overall aesthetic appeal rather than the attractiveness of the model, then a leftward bias would be expected in modeling photographs. By asking the same group of individuals to make their selections based on the two sets of criteria, we can assess both the relative attractiveness of the two sides of the face and whether overall image appeal differs from the specific evaluation of facial attractiveness.

To assess the influence of image selection factors on posing bias, future research could extend the magazine cover shoot scenario to the role of art director rather than the role of cover model. Participants would be presented with pairs of rightward and leftward poses (counterbalanced with their mirror-imaged pairs) and asked to select which image best matches two selection criteria: 1) Which image is more aesthetically pleasing? 2) Which image best emphasizes the model's attractiveness? If the right cheek is more attractive, but modeling photographs are selected based on overall aesthetic appeal, then right-cheek images (whether presented in their original or mirror-reversed orientation) should be selected more often than left cheek poses when assessing the overall attractiveness of the model, but left-cheek images should be selected as being more aesthetically pleasing overall.

Shifting from posing biases to seating biases, Experiment 5 was designed to assess whether the seating biases observed when seats are selected from paper seating charts accurately reflected real-world seating behaviour. The rightward bias observed for theatre-patrons in a real movie theatre setting confirmed the rightward seating bias. Experiment 6 was designed to test the competing predictions of Karev's (2000) expectancy hypothesis and Weyers et al.'s (2006) motor asymmetry hypothesis. Consistent with Karev's prediction, a leftward seating bias was observed for classroom seating, where processing demands favour the left hemisphere.

Taken together, these four experiments provide a body of evidence that demonstrates an influence of hemispheric lateralization on real-world behaviour, beyond the basic performance advantages that receive the focus of most laterality studies. The asymmetries in how we process the information in our environment in turn influence how we interact with that environment. Although Weyers et al.'s motor asymmetry hypothesis provides a simple and elegant explanation to the right side seating bias for movie theaters, it fails to account for the leftward seating bias encountered in the classroom setting. It does appear that seating behaviour is influenced by expected processing demands based on the environmental context. This pattern suggests that asymmetry in cognitive functioning influences behaviour at the macroscopic, global level.

I demonstrated that picking a seat in a theatre is more complicated than a simple motor bias to turn or move towards the right; however, one cannot discount this influence as playing a role. It is more likely that the biases we observe in daily life are the product of a set of competing influences. Perhaps a left ear bias for emotional content competes with a right ear bias for verbal content. In addition, visual biases for emotional

information, words, faces, and attention are all competing for influence as well. Add to this motor biases from turning, walking, and fine motor control, plus more conscious biases such as preferences for aisle seats or aversions to cell-phone users or loud popcorn-chewers, and the seating biases we observe become far more complicated. Further research examining the behavioural consequences of lateral asymmetries should specifically assess the degree and direction of asymmetry for visual attention, facial processing, emotional processing, and language within individuals and then compare it to their specific behavioural biases.

For example, future research on seating biases should include assessing whether a consistent relationship exists between right-hemisphere lateralization for spatial or emotional processing and a rightward seating preference in a movie theatre. If seating preference is governed by our expectation of processing demands, then the direction of lateralization for the specific processing demands of an event should predict seating preference, with a greater degree of lateralization predicting more stable seating biases. Confirming that rightward seating preference in a movie theater is associated with right-hemisphere dominance for facial, emotional, or visuospatial processing would provide a solid source of evidence for the influence of expected processing demand on seating behaviour. Further convincing support for this position would be found in individuals showing reversed or atypical patterns of lateralization. If hemispheric dominance for spatial or emotional processing are reversed in some individuals (showing left hemispheric dominance), then those individuals should show reversed seating preferences (e.g. leftward seating preference in a movie theatre). Confirmation of this pattern would

demonstrate a clear connection between the pattern of functional lateralization and behavioural biases.

Additionally, at the core of Karev's (2000) hypothesis is the assumption that seating position preferentially directs information to the dominant hemisphere for processing; this results in faster, more efficient processing of the expected content. If seating position does influence processing efficiency, then people seated on the right side of a theatre should show faster and more accurate emotional and visuospatial processing performance compared to those seated on the left. This assertion could be tested by evaluating whether processing efficiency results in faster and more accurate performance on visuospatial or emotional processing tasks for people seated to the right of a stimulus display screen compared to people seated to the left. If Karev's proposal is correct, then an overall processing efficiency advantage should be observed for right-side sitters compared to left-side sitters for right-hemisphere dominant processing tasks such as facial recognition or visual search. Conversely, if other influences such as turning biases or the influence of external factors are the primary biasing force, then the task performance should not vary systematically between left- and right-side sitters.

In light of the results presented here, can any of the evolutionary explanations for cerebral lateralization be discredited? No, they cannot. The greater picture of related and independent processes must be addressed in developing an evolutionary account rather than laying blame or credit on a single function or subset of functions. These accounts must also consider both individual- and population-level laterality effects. Population-level biases can be observed without all individuals showing a similar lateral asymmetry, and atypical laterality profiles in individuals are more common than the population-level

modal model would suggest. Similarly, when evaluating the influences of cerebral lateralization on everyday behaviours, one cannot over-simplify and base our accounts on a single lateralized influence. The relative power of each contributing influence must be established in order to fully understand what produces our complex patterns of behavioural biases.

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10. Appendix A

PARTICIPANT QUESTIONNAIRE ID#____

Age: _____

Sex: **M** **F** (circle one)

If you are a student, what is your major? _____

What was the **first** language you learned as a child? **English** **French** **Chinese** **Other:**_____

Do you have any hearing impairments? **Yes** **No**

Do you have any visual impairments (including colourblindness)? **Yes** **No**

What colour are your eyes? **Blue** **Brown** **Green** **Hazel** **Violet** **Other:**_____

What is your natural hair colour? **Blonde** **Brown** **Black** **Red** **Auburn** **Other:**_____

Do you have any primary **biological** relatives (i.e. mother, father, brother, or sister) who are left-handed? **Yes** **No** **Don't Know**

Do you have any **biological** extended family members (i.e. grandparents, biologically related aunts and uncles) who are left-handed? **Yes** **No** **Don't Know**

Please list any medications (including oral contraceptives) that you are currently taking:

Instructions: Please indicate your hand preference for the following activities by circling the appropriate response. If you **always** (i.e., 95% or more of the time) use one hand to perform the described activity, circle **Ra** or **La** (for **right always** or **left always**). If you **usually** (i.e., about 75% of the time) use one hand circle **Ru** or **Lu**, as appropriate. If you use both hands **equally often** (i.e., you use each hand about 50% of the time), circle **Eq**.

1. With which hand would you use a pair of tweezers?	**La**	**Lu**	**Eq**	**Ru**	**Ra**
2. With which hand would you use a paintbrush to paint a wall?	**La**	**Lu**	**Eq**	**Ru**	**Ra**
3. Which hand would you use to pick up a book?	**La**	**Lu**	**Eq**	**Ru**	**Ra**
4. With which hand would you use a spoon to eat soup?	**La**	**Lu**	**Eq**	**Ru**	**Ra**
5. With which hand would you use the eraser on the end of a pencil?	**La**	**Lu**	**Eq**	**Ru**	**Ra**
6. Which hand would you use to pick up a piece of paper?	**La**	**Lu**	**Eq**	**Ru**	**Ra**
7. Which hand would you use to draw a picture?	**La**	**Lu**	**Eq**	**Ru**	**Ra**
8. Which hand would you use to hammer a nail?	**La**	**Lu**	**Eq**	**Ru**	**Ra**
9. Which hand would you use to insert a plug into an electrical outlet?	**La**	**Lu**	**Eq**	**Ru**	**Ra**
10. Which hand would you use to throw a ball?	**La**	**Lu**	**Eq**	**Ru**	**Ra**
11. In which hand would you hold a needle while sewing?	**La**	**Lu**	**Eq**	**Ru**	**Ra**
12. Which hand would you use to turn on a light switch?	**La**	**Lu**	**Eq**	**Ru**	**Ra**
13. Which hand do you use for writing?	**La**	**Lu**	**Eq**	**Ru**	**Ra**
14. Which hand would you use to saw a piece of wood with a hand saw?	**La**	**Lu**	**Eq**	**Ru**	**Ra**
15. Which hand would you use to open a drawer?	**La**	**Lu**	**Eq**	**Ru**	**Ra**

Continued On Other Side

16. Is there any reason (e.g., injury) why you have changed your hand preference for any of the above activities? **YES** **NO**

17. Have you been given special training or encouragement to use a particular hand for certain activities? **YES** **NO**

18. If you have answered YES to either Questions 16 or 17, please explain.

Instructions: Please indicate your foot preference for the following activities by circling the appropriate response. If you **always** (i.e., 95% or more of the time) use one foot to perform the described activity, circle **Ra** or **La** (for **right always** or **left always**). If you **usually** (i.e., about 75% of the time) use one foot circle **Ru** or **Lu**, as appropriate. If you use both feet **equally often** (i.e., you use each hand about 50% of the time), circle **Eq**. Please do not simply circle one answer for all questions, but imagine yourself performing each activity in turn, and then mark the appropriate answer.

19. Which foot would you use to kick a stationary ball at a target straight ahead?	**La**	**Lu**	**Eq**	**Ru**	**Ra**
20. If you had to stand on one foot, which foot would it be?	**La**	**Lu**	**Eq**	**Ru**	**Ra**
21. Which foot would you use to smooth sand at the beach?	**La**	**Lu**	**Eq**	**Ru**	**Ra**
22. If you had to step up onto a chair, which foot would you place on the chair first?	**La**	**Lu**	**Eq**	**Ru**	**Ra**
23. Which foot would you use to stomp on a fast-moving bug?	**La**	**Lu**	**Eq**	**Ru**	**Ra**
24. If you were to balance on one foot on a railway track, which foot would you use?	**La**	**Lu**	**Eq**	**Ru**	**Ra**
25. If you wanted to pick up a marble with your toes, which foot would you use?	**La**	**Lu**	**Eq**	**Ru**	**Ra**
26. If you had to hop on one foot, which foot would you use?	**La**	**Lu**	**Eq**	**Ru**	**Ra**
27. Which foot would you use to help push a shovel into the ground?	**La**	**Lu**	**Eq**	**Ru**	**Ra**
28. During relaxed standing, most people have one leg fully extended for support and the other slightly bent. Which leg do you have fully extended first?	**La**	**Lu**	**Eq**	**Ru**	**Ra**

29. Is there any reason (i.e. injury) why you have changed your foot preference for any of the above activities? **Yes** **No**

30. Have you ever been given special training or encouragement to use a particular foot for certain activities? **Yes** **No**

31. If you have answered YES for either question 29 or 30, please explain:

The experimenter will complete question 32:

32. Eyedness **Left** **Right**

11. Appendix B

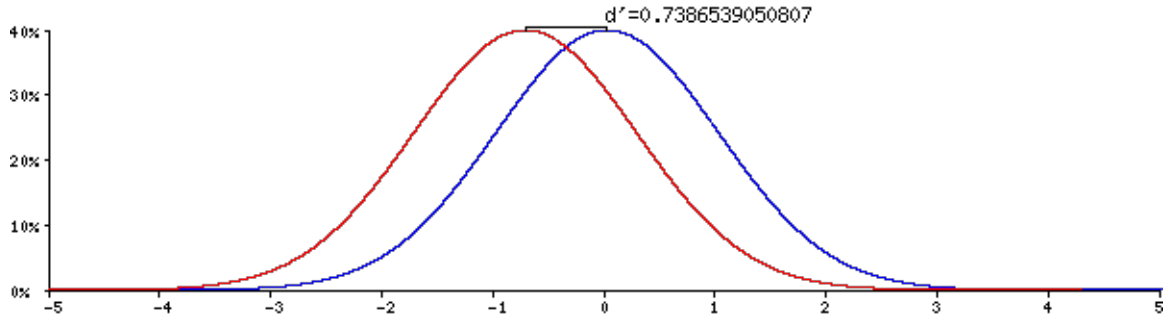
Signal detection for Unfamiliar Melody Recognition Task

Basic Variables:

Targets	2156
Noise	10780
Hit Proportion	51.25%
False Alarm Proportion	23.97%
Percent Correct / p(c)	71.90%
Percent Correct - *Std. Err.*	0.77%

Signal Detection Theory Variables:

d'	0.739
d' - *Std. Err.*	0.000
c	0.338
c - *Std. Err.*	0.000
c'	0.457
β_G	1.284
$ln(\beta_G)$	0.250



Given the relatively small difference between the means of the signal present and signal absent distributions (*d'* = .739), in combination with the low criterion value (*c* = .338) and unequal distribution of correct target present and target absent trials, it is most likely that participants developed a greater tendency to reply "no" on a given trial. This suggests that performance on the melody recognition task did not differ significantly from chance.

12. Appendix C

Female Subsample

A subset of the female headshots was randomly selected to create an equal sample size for comparison with the male headshots (male = 80 images, female = 80 images). A univariate ANOVA was used to examine the influence of subject sex (male, female) and body visibility (head, head and shoulders, full torso) on posing direction. There was no difference in posing bias between males and females; $F(1, 154) = .215$, $p = .643$, partial $\eta^2 = .001$. Similarly, no influence of body visibility was found; $F(2, 154) = .491$, $p = .613$ partial $\eta^2 = .006$. The interaction between sex and body visibility was also not significant; $F(2, 154) = 1.537$, $p = .218$ partial $\eta^2 = .020$.